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Estimating relative risk of within-lake aquatic plant invasion using combined measures of recreational boater movement and habitat suitability

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Abstract

Effective monitoring, prevention and impact mitigation of nonindigenous aquatic species (NAS) relies upon the ability to predict dispersal pathways and receiving habitats with the greatest risk of establishment. To examine mechanisms affecting species establishment within a large lake, we combined observations of recreational boater movements with empirical measurements of habitat suitability represented by nearshore wave energy to assess the relative risk (RR) of Eurasian watermilfoil (*Myriophyllum spicatum*) establishment. The model was evaluated using information from a 17 year (1995-2012) sequence of *M. spicatum* presence and absence monitoring. *M. spicatum* presence was not specifically correlated with recreational boater movements; however its establishment appears to be limited by wave action in Lake Tahoe. Of the sites in the "High" risk category (n=37), 54% had current or historical infestations, which included 8 of the 10 sites with the highest RR. Of the 11 sites in the "Medium" risk category, 5 had current or historical *M. spicatum* populations. Most (76%) of the sites in the "Low" risk category were observed in locations with higher wave action. Four sites that received zero boater visits from infested locations were occupied by *M. spicatum*. This suggests that the boater survey either represents incomplete coverage of boater movement, or other processes, such as the movement of propagules by surface currents or introductions from external sources are important to the establishment of this species. This study showed the combination of habitat specific and dispersal data in a relative risk framework can potentially reduce uncertainty in estimates of invasion risk.

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Introduction

Predicting establishment for nonindigenous aquatic species (NAS) remains one of the greatest challenges for invasion ecologists yet is a key element for effective ecosystem monitoring and management. Assessing the risk of establishment requires an understanding of the number of individuals introduced to a particular area over time (i.e., propagule or colonization pressure) and characteristics of the receiving environment (Lockwood, Cassey & Blackburn, 2005). Where propagule pressure is high and habitat is suitable for a species to survive and reproduce, the risk of establishment and growth is substantial (Von Holle & Simberloff, 2005; Drake & Jerde, 2009).

Propagule pressure is difficult to measure directly for most aquatic species. Within aquatic ecosystems, boat movement as well as dispersal through natural currents contribute to the propagation and spread of aquatic species (Mosisch & Arthington, 1998; Beletsky et al., 2007; Clarke Murray, Pakhomov & Therriault, 2011). Both fragments and established populations of invasive seaweed (*Caulerpa taxifolia*) have been found in greater abundances in estuaries with high rates of recreational boating compared to areas with less recreational boating (West et al., 2009). Hull fouling associated with commercial or recreational activities is a well-known dispersal vector for both marine and freshwater introductions (Johnson & Carlton, 1996; Mineur, Johnson & Maggs, 2008; Clarke Murray, Pakhomov & Therriault, 2011). The exchange and discharge of ballast water has also been shown to increase secondary spread rates within the Great Lakes (Carlton, 1985; Sieracki, Bossenbroek & Faisal, 2013). Finally, advective movement via surface currents have also been found to increase the spread of both fish and invertebrate species within large lakes (Beletsky et al., 2007; Hoyer et al., 2014). While a lot of information exists regarding the spread of species within aquatic systems, the specific relationship between human-mediated and natural dispersal of species is largely unknown.

The focus of the current study was Eurasian watermilfoil (*Myriophyllum spicatum* L., hereafter EWM) a freshwater macrophyte species native to Europe, Asia and Northern Africa and introduced to North America in the 1940's (Couch & Nelson, 1985). In North America, EWM impacts native species (Boylen, Eichler & Madsen, 1999) and has unwanted effects on ecosystem services (Eiswerth, Donaldson & Johnson, 2000; Halstead et al., 2003; CAST, 2014). Widespread dispersal occurred after its initial introduction in North America, as EWM was a popular aquarium and trade species, and also planted into lakes and streams—spreading through water currents to connected waterways (Aiken et al., 1979; Madsen, Eichler & Boylen, 1988). Recreational boats have also been implicated as a dispersal vector for freshwater aquatic plants (Johnstone, Coffey & Howard-Williams, 1985). EWM is estimated to have arrived in this study system, Lake Tahoe, CA-NV [USA] in the 1960's (Kim & Rejmankova, 2001), and by 2012 had spread to over 20 sites within the lake, covering approximately 85 acres (Fig. 1).

The dispersion of EWM within Lake Tahoe is a complex process with multiple interacting components. Fragments are created when boat propellers cut the plant, when mechanical harvesting occurs (a non-chemical control activity in the lake), and naturally due to the plant's phenology. EWM has survived and produced roots up to six weeks post fragmentation (Jerde et al., 2012; Mcalarnen et al., 2012). Long distance dispersal within the lake then depends on transport mechanisms between areas where EWM is established and areas where it is not. This may include the movement of fragments across open waters or laterally within nearshore regions.

Once viable fragments reach a novel habitat, various environmental parameters such as temperature, energetics of surface waves, and sediment composition determine if new EWM colonies will become established (Smith & Barko, 1990; Martin & Valentine, 2012). EWM grows best on fine textured inorganic sediments (Barko & Smart, 1986) and grows relatively poorly on highly organic sediments and on coarse substrates (sand and gravel) (Smith & Barko, 1990). The intensity of wave action and water movement are also important factors for EWM establishment; stimulating both abundance at low to moderate velocities, but reducing growth at higher velocities (Schutten & Davy, 2000; Madsen et al., 2001; Martin & Valentine, 2012). As invasion success is dependent on multiple factors (e.g., transport, propagule pressure, habitat suitability), combining assessments of these factors, when possible, should improve estimates of risks for further spread and establishment.

Because it is difficult to observe an accurate relationship between propagule pressure and invasion risk when habitat suitability is different across sites, one approach is to include relative measures of individual survival and propagule pressure to develop a prediction framework (Herborg et al., 2007; Jerde & Lewis, 2007). For example, gravity models have used recreational boater movements to estimate relative abundance of human-transported NAS (Schneider, Ellis & Cummings, 1998; Bossenbroek, Kraft & Nekola, 2001; Muirhead & Macisaac, 2005), but have failed to incorporate the characteristics of the receiving habitat into predictions of establishment likelihood. Relative measures of species survival have been estimated using habitat matching models that compare species origins and putative destinations on a global scale (Drake & Bossenbroek, 2004; Herborg et al., 2007). We seek to combine measures of propagule pressure and habitat suitability within a lake, in order to establish a framework that can be used for managers tasked with minimizing the impact of invasion that is already ongoing.

This study assesses the relative risk of invasion spread within a single freshwater lake (Lake Tahoe) by examining two components of EWM establishment: the physical properties of recipient habitats, and human-mediated propagule pressure via recreational boating trips between these habitats. We used direct measures of boater visitation frequency to approximate propagule pressure. Intensity of wave action at nearshore locations in Lake Tahoe was used to categorize relative risk into three categories (high, medium, low) and identify areas most vulnerable to recreational boat-mediated introduction of EWM. We hypothesized that if wave height and propagule pressure are working in concert to determine establishment, then more sites in the high-risk category should be invaded than in the medium and low risk categories. Within a category, if propagule pressure is driving establishment, then sites with relatively more risk should be more likely to have been invaded.

Materials and Methods

Site description

Lake Tahoe is a large (surface area: 497 km^2, max depth 501 m), oligotrophic lake located in the Sierra Nevada between California and Nevada USA at a subalpine elevation of 1898 m. The Tahoe basin's granitic geology, the lake's large volume (150 km^3) and small watershed (800 km^2) explain the low nutrient concentrations and primary productivity rates (Goldman, 1988) . While native plant species such as Andean milfoil (*M. quitense*), Canadian waterweed (*Elodea* *canadensis*), coontail (*Ceratophyllum demersum*), Richardson's pondweed (*Potamogeton richardsonii*) and leafy pondweed (*Potamogeton foliosus*) are found in Lake Tahoe, the nonnative EWM and curlyleaf pondweed (*P. crispus*) dominate much of the submersed aquatic plant community, particularly in the constructed marinas at the south end of the lake. Lake Tahoe is subject to intense recreational pressure, with over 3 million people visiting and over 20,000 trailered boats launched into the lake each year.

Distribution of Eurasian watermilfoil populations and recreational boater survey

Lake surveys to determine Eurasian watermilfoil distribution, 1995 – 2012

Whole lake surveys for EWM presence and absence were carried out annually in Lake Tahoe from 1995 to 1997 and in 2000, 2003, 2006 and 2012. A two to three person boat crew circumnavigated the nearshore zone, including marinas and other embayments, and visually inspected below the water surface for aquatic macrophytes from the vessel. If vegetation was spotted, a double-edged rake was thrown into the vegetation or divers snorkeled underwater to retrieve samples for species identification in the laboratory (Anderson & Spencer, 1996). In 2012 divers snorkeled or used SCUBA amongst vegetation to make *in situ* identification (K. Boyd, pers. comm. 2014).

Recreational boater survey

To determine the pathways of Lake Tahoe boaters, individuals (N=778) were interviewed 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. On any given date, interviews were conducted for an 8-

10 hour period between 8 A.M. and 6:00 P.M. The interview consisted of ten questions and lasted approximately 5–10 minutes. Questions relevant to this study pertained to the boater's launch origination and trips made between nearshore zones within the lake. The set of originations and destinations were defined by responses given by boaters, with as few as 1 and as many as 5 origination and destination combinations per boater collected. Each origination and destination combination was counted as one trip, and when the origination was from a site that contained EWM, that trip constituted one potential propagule. This measurement of visitation to each boater destination site from a set of infested locations is referred to as B.

Habitat characterization

Wave action

To gauge the amount of energy or wave action in nearshore zones in Lake Tahoe, change in vertical pressure was measured using submersed depth pressure sensors (RBR DR-1050, accuracy ±0.05%) at 13 locations around the lake (Fig. 1). The sensor locations were distributed around all sides of the lake and were chosen to capture nearshore wave action caused by prevailing wind patterns (Schladow et al., 2012). Each sensor was placed at approximately the same depth (3 m) and set at a 1 second sampling interval for a period of 14 days from July through September 2006. Because there were only four sensors and a limited field period, measurements were taken continuously at the northern end of the lake (site CBI) with a single logger, and three other loggers were moved every 14-day sampling period. The continuous measurements taken at CBI were used to estimate significant wave heights (H_s, or the highest 1/3 of all waves measured) during the weeks for which a site did not have a logger present. This estimation was done 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 was calculated using the following pressure to wave height conversions:

$$pressure = p - Atmospheric\ pressure\ (dBar)\ , \qquad \text{Equation 1}$$

where p = pressure reading from the sensor (dBar), and atmospheric pressure was the calibration for high elevation conditions at Lake Tahoe (1897 m). The conversion of pressure into depth was described by the following equation:

$$depth(m) = \frac{pressure}{g\rho}\ , \qquad \text{Equation 2}$$

where g is a gravitational constant (0.980665 m s^{-2}) and ρ (1.0 g mL^{-3}) is water density. 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 and represented the temporal variability over the entirety of the sampling period for each site (Dean & Dalrymple, 1991). For each of the locations identified by recreational boaters, wave height characterizations were assigned based on proximity to the nearest pressure sensor measurement.

Estimating Relative Risk

We used relative measures of boater visitation from an infested site (*B*), to assess invasion risk of EWM within Lake Tahoe. After Jerde and Lewis (2007), we calculated the relative ratio (*RR*) of *B* for invasion of location X relative to *B* for invasion of location Y, where location Y was the location with the lowest (non-zero) B, for each site. Simply, RR was the proportion of boater visitation (B_X) for a site, relative to the B_Y for the least visited site:

$$RR = \frac{B_X}{B_Y} \qquad \text{Equation 3}$$

As EWM establishment has been shown to be limited by wave action (Schutten & Davy, 2000; Martin & Valentine, 2012), we further refined the relative risk evaluation based on empirical measurements of wave height. This serves to improve the ability to prioritize specific sites for surveillance by further categorizing relative risk by high, medium and low habitat suitability. Specifically, risk categories were divided into three groups according to their maximum wave height (H_{max}) as measured during the June - August, 2006 period in Lake Tahoe: "High risk" (<0.2 m) "Medium risk" (0.2 - 0.3 m) or "Low risk" (>0.3 m). If the sites were in different risk categories, then relative risk comparisons were not valid owing to the unknown relationship between H_{max} and EWM establishment.

We used a chi-squared test to determine whether there were differences between the frequencies of invasion for the "High", "Medium", and "Low" risk categories. If there were no statistically significant differences between these categories, then we would proceed to test the explanatory power of the relative risk across all sites. However, if the contingency table was significant and cell frequencies are justifiably interpretable, then logistic regression would be performed on each category (High, Medium, and Low) with number of boater visits as the explanatory variable. All analyses were carried out using R (v 2.13.0).

RESULTS

Eurasian watermilfoil survey

In 1995, there were 13 nearshore sites in Lake Tahoe with EWM presence. The number of sites with EWM presence slowly increased, with 17 sites observed in 2000, 22 sites in 2003 and 26 sites in 2005. In 2011 there were 23 sites with EWM presence, and the last survey in 2012 also showed a decrease in the number of sites, with a total of 17 occupied by EWM (Fig. 2), with a total coverage of approximately 85 acres. The decrease in number of sites in 2011 and 2012 relative to previous years is a result of management (bottom barriers, dredging) and/or other causes of extirpation of localized populations (K. Boyd pers. comm. 2014).

Recreational boater survey

There were a total of 65 sites named by the 778 interviewed recreational boaters as destinations within Lake Tahoe (Fig. 2). There were 1756 origination–destination trips and the most visited sites included Emerald Bay (a popular scenic destination; N = 273 trips) and Tahoe Keys (a destination with amenities e.g., gas, food, launch ramp; N = 214). Both of these sites have established EWM populations; however the Tahoe Keys infestation is much greater, with dense stands reaching the water surface and directly adjacent to moored boats and in boat traffic lanes. Other popular sites visited were those with amenities (restaurants, gas stations) or are known as popular places to recreate. There were 769 origination-destination trips from locations with EWM. A point biserial correlation coefficient was computed to assess the relationship between the presence of EWM (including extirpated populations) and recreational boater visitation. There was no significant correlation between the two variables ($r_{pb} = 0.22$, df = 63, p = 0.08).

Physical Habitat and Relative Risk categorization

Similar to Lake Tahoe nearshore wave heights recorded during 2008-2009 summer and winter periods (which included one winter storm) (Schladow et al., 2012), wave heights measured in this study ranged from 0 to 0.5 m (Table 1). In general, the eastern shore of Lake Tahoe receives more wave action than the west shore of the lake (Schladow et al., 2012). Pressure sensor measurements also confirmed this to be true during the summer of 2006; the highest maximum wave heights recorded were on the east or northeast shore at CR, CBI, RHP, SH and ZPH (Table 1). Of 13 sites measured, five sites had an $H_{max} < 0.2$, four sites were between 0.2 and 0.3, three were 0.3 or greater and one sensor malfunctioned during its deployment at location DLB and was not included. This breakdown was used to define the relative risk categories.

There was a significant association between risk category and frequency of EWM presence (χ^2=8.66, df = 2, $p = 0.013$; Table 2). Of the 37 sites in the "High" risk category, 54% have current or historical infestations of EWM, including 8 of the 10 sites with the highest RR in this risk category. Of sites in the "High" risk category, 35% had $B = 0$, indicating no visitation by boaters originating from sites with EWM. Of the 11 sites in the "Medium" risk category, 5 have either current or historical EWM populations and 9 sites have $B > 0$. Most of the sites in the "Low" risk category are located on the east or northeast shore (e.g., the locations with higher wave action), and only two of them have current or historical EWM populations. However, both of these populations are in protected areas (e.g., behind rock cribs or within a marina), and were not exposed to wave action of the other 15 sites. Thus, these locations may be considered as high energy (e.g., low risk) environments that are overcome by protective barriers.

There was only adequate power for logistic regression analyses within the high risk category, which indicated that RR was not a reasonable predictor of EWM presence ($z = 0.903$, $p= 0.367$, $df = 36$). When risk categorizations are removed and RR was considered over all sites, it was also not a reasonable predictor of EWM presence ($z = 1.386$, $p = 0.166$, $df = 64$).

Discussion

Similar to previously published assessments of EWM establishment at the landscape scale (Buchan and Padilla 2000; Rothlisberger and Lodge 2011), we have found that propagule pressure as represented by recreational boater visitation was not a significant explanatory factor of its presence within a lake. Further, characteristics of the receiving habitat, e.g., wave action, were found to be a limiting factor for EWM establishment in Lake Tahoe. Here, applying the relative risk assessment using nearshore measurements of wave action increased the rate of true positives, relative to the "high" risk (e.g., low wave action) category, and decreased the rate of false positives relative to the "low" risk (e.g., high wave action) category. In this sense, integrating habitat data into a relative risk assessment framework decreased the uncertainty associated with forecasting species establishment. However, the extent to which boater movement is a singular useful predictor of EWM in Lake Tahoe is not clear. While recreational boats may certainly play a role in the release and movement of EWM, the plant’s distribution may be more dependent on alternative dispersal vectors (e.g. wind-driven surface currents), variation in temporal scales, or habitat limitations.

There were four sites (23% of those with infestations) where boater visitation was 0, yet populations of EWM have been present in those locations for a majority of the invasion record. This indicates that either the boater survey data did not accurately represent visitation, or that another physical process such as the movement of propagules by surface currents is important. It possible that a fragment of EWM 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 also likely that a boat travels through a high growth EWM area within a nearshore zone or marina, and moves fragments out to the open lake. In this scenario, boaters may not deliver a propagule to other nearshore sites, but rather may liberate plant fragments from protected areas out into the lake, where they may be susceptible to advective transport to nearshore zones by water currents.

However, it is possible that recreational boating played an important role in the delivery of invasive plants to popular and scenic sites such as Emerald Bay. Emerald bay is one of the few non-marina sites that contain EWM in the lake. It is also the most highly visited area by boaters in Lake Tahoe; over 70% of surveyed boaters visited this location. The predominant south shore winds and water flows move eastward (Schladow et al., 2012; the opposite direction of Emerald Bay from most established EWM populations; see Fig. 1). The abrupt presence of the recently established non-native species, curlyleaf pondweed, at this Emerald Bay indicates that some sort of long distance dispersal mechanism may be supporting the establishment of species in this area.

Wave action has been cited as an important factor for EWM growth and establishment in Lake Tahoe and elsewhere (Walter, 2000; Madsen et al., 2001; Martin & Valentine, 2012). The energetics of highly wavy sites such as CR, ZPH and SH along the eastern shore combined with EWM absence (with the exception of locations where there are protective rock cribs or marina structures) supports this notion. However, measurements of nearshore wave action presented here provided only a coarse estimate of the relationship between EWM distribution and nearshore energetics, which may affect the precision of the model estimates. This coarseness is due in part to the short duration of empirical data collection (e.g., 14 days per probe and a two month overall period) at each site and the interpolation of the 13 site-specific observations to broader regions around the lake. These issues could be refined in the future through the use of more pressure sensors over a longer time period to capture inter-seasonal variability as well as the provision of higher resolution estimates of nearshore energy. However, the observations collected in this study capture the range of wave heights measured by Schladow et al. (2012) in Lake Tahoe in both summer and winter periods, including summer and winter storms. In addition, Schladow et al., (2012) simulated nearshore wave action using a high resolution Steady-State Spectral Wave Model, STWAVE (Smith, 2001), which produced the same spatial patterns associated with nearshore zones observed in the data presented herein.

Temporal lags associated with the expansion of EWM within Lake Tahoe may also be indicative of why some sites with high relative risk estimates do not have established EWM populations. We propose that these lags may be attributed to the lake's trophic status. EWM was first discovered in the Lake Tahoe Keys development over 60 years ago (Eiswerth, Donaldson & Johnson, 2000). Currently, the plant is established in only 17 locations around the 116 km lake perimeter, with an abundance of potentially suitable (e.g., sandy sediments and protected embayment) habitats remaining unoccupied. Oligotrophic systems, such as Lake Tahoe, often are characterized by low benthic taxon richness (Declerck et al., 2005), which may make these communities less resistant than more diverse communities to species invasions (Stachowicz et al., 2002). Properties of oligotrophic systems that contribute to low taxon richness, such as low nutrient conditions, temperatures or high UV exposure (Tucker et al., 2010) can potentially present the same barriers to somatic growth, spread and establishment for EWM in this system. However, Lake Tahoe's benthic community is currently undergoing significant environmental change (Caires et al., 2013), and eutrophication favors the success of colonists (Christie, Fraser & Nepszy, 1972). Indeed, Lake Tahoe has recently experienced increased disturbance through nearshore development, temperature warming the establishment of other NAS (e.g., Asian clam, signal crayfish and various warmwater fishes) and losses in water transparency (Goldman, 1988; Frantz & Cordone, 1996; Chandra et al., 2005; Kamerath, Chandra & Allen, 2008; Coats, 2010; Wittmann et al., 2012). These stressors are likely to alter ecosystem dynamics that may affect the establishment of species such as EWM.

Future directions

There are many unknowns associated with the establishment of species, which often leaves managers having to react to, rather than prevent, new infestations of NAS within ecosystems. Here, we have developed an approach to reduce the uncertainty associated with identifying site-specific establishment risk and the subsequent development of surveillance or other management programs within an ecosystem or management unit. We propose that this framework can not only be applied to within-lake monitoring programs, but also to a wide range of species over multiple scales (e.g., within lake, regional or national) in order to identify risk, surveillance programs and prioritize control strategies required for effective NAS management (e.g., Herborg et al., 2007). The ability to apply this kind of risk framework may be attributed to the increased availability of species- or system-specific data. As species invasions have increased, so too has the collection of relevant monitoring and data associated with NAS. Freely available resources that describe species dispersal pathways (e.g., the 100th Meridian Initiative Recreational boater database, National Ballast Information Clearing House) combined with field measurements of physical or biological data (e.g., NOAA National Climatic Data Center, USGS Nonindigenous Aquatic Species Database) can be compiled to build an information rich source of risk assessment to identify regions vulnerable to unwanted species establishments using methods or strategies proposed here.

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Tables

ID	Location Name	Lat	Long	H_s	H_{max}	H_{rms}	Risk
BWM	Boatworks Marina	39.171	-120.137	0.006	0.027	0.003	High
KBG	Garwoods	39.225	-120.083	0.004	0.031	0.002	High
CRM	Camp Richardson	38.939	-120.039	0.019	0.113	0.011	High
LFL	Lake Forest Launch	39.181	-120.120	0.013	0.128	0.008	High
EPM	Elks Point	38.984	-119.957	0.020	0.181	0.012	High
ZPH	Zephyr Cove	39.007	-119.950	0.027	0.208	0.017	Medium
RHP	Round Hill Pines	38.990	-119.954	0.025	0.213	0.016	Medium
RUB	Rubicon Bay	39.002	-120.102	0.018	0.218	0.010	Medium
SPE	Sugar Pine/Ehrman	39.060	-120.113	0.034	0.253	0.021	Medium
SH	Sand Harbor	39.201	-119.931	0.029	0.294	0.019	Low
CBI	Crystal Bay/Incline	39.248	-119.989	0.029	0.377	0.019	Low
CR	Cave Rock	39.042	-119.949	0.059	0.537	0.040	Low

Table 1. Location and position of pressure sensors in Lake Tahoe to measure nearshore wave heights June - August, 2006. H_s = Significant Wave Height, H_{max} = Maximum Wave Height, H_{rms} = Root mean square Wave Height, all represented in meters (m). Risk = Category of Eurasian watermilfoil risk of establishment based on H_{max}; High <0.2, 0.2< Medium <0. 3, and Low >0.3 m.

High Risk (Low Wave Action)

Site	B	RR(B)
EmeraldBay*	0.22	169
LakeForest	0.16	124
TahoeKeys*	0.10	79
CampRich†	0.08	58
ElDorado*	0.04	27
Sunnyside†	0.03	22
BaldwinBeach†	0.02	15
TahoeCity*	0.01	10
Garwoods	0.01	7
HurricaneBay	0.00	2
KivaBeach*	0.01	5
KingsBeach	0.01	4
SkiRun*	0.01	4
SouthShore*	0.01	4
Stateline*	0.01	4
SkiBeach	0.00	2
TimberCove*	0.00	2
CarnelianBay	0.00	1
Cascade	0.00	1
LarsonsBeach	0.00	1
LesterBeach	0.00	1
PopeBeach*	0.00	1
TahoeMeadows*	0.00	1
TahoeTavern†	0.00	1
AgateBay	0.00	0
Chinquapin	0.00	0
DollarPoint	0.00	0
ElksPointBeach*	0.00	0
HighSierraBoatCo	0.00	0
Lakeland*	0.00	0
NevadaBeach*	0.00	0
SierraBoatCo	0.00	0
SkylandiaBeach	0.00	0
TahoeFlats†	0.00	0
TahoePark†	0.00	0
TahoePines	0.00	0
TahoeVista	0.00	0

Medium Risk (Medium Wave Action)

Site	B	RR(B)
MeeksBay*	0.05	14
ZephyrCove†	0.04	11
RubiconBay	0.03	9
DLBliss	0.02	5
SugarpinePoint	0.02	5
Obexers†	0.02	4
Homewood†	0.01	3
RoundHillPines*	0.01	2
ChambersBeach	0.00	1
MarlaBay	0.00	0
Tahoma	0.00	0

Low Risk (High Wave Action)

Site	B	RR(B)
SandHarbor	0.04	16
CaveRock	0.02	6
SkunkHarbor	0.01	4
InclineVillage	0.01	2
Hyatt	0.00	1
SecretHarbor	0.00	2
DeadMansPoint	0.00	1
ThunderbirdLodge	0.00	1
CalNeva	0	0
ChimneaBeach	0	0
CrystalBay*	0	0
GlenBrook	0	0
HiddenBeach	0	0
LoganShoals†	0	0
Lynbrook	0	0
SnakeHarbor	0	0
SpeedboatBeach	0	0

Table 2. Proportion of boater visits from sites with Eurasian milfoil (B; Total number of trips from infested locations, N = 769), and RR(B) or Relative Risk based on B for 65 nearshore sites

in Lake Tahoe, USA. RR is relative to site differentiation as determined by measurements of nearshore wave action. *Currently infested with Eurasian milfoil, †Historical infestation of Eurasian milfoil.

Figures

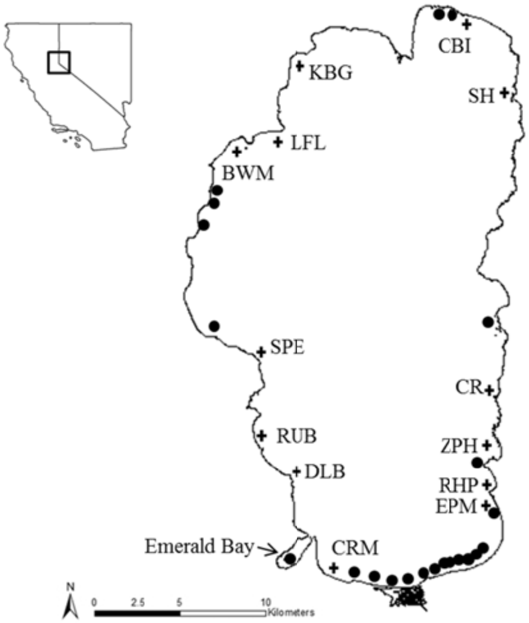

Figure 1. Lake Tahoe, CA-NV. Circles indicate Eurasian watermilfoil presence as of 2012. Crosses indicate wave action measurement sites.

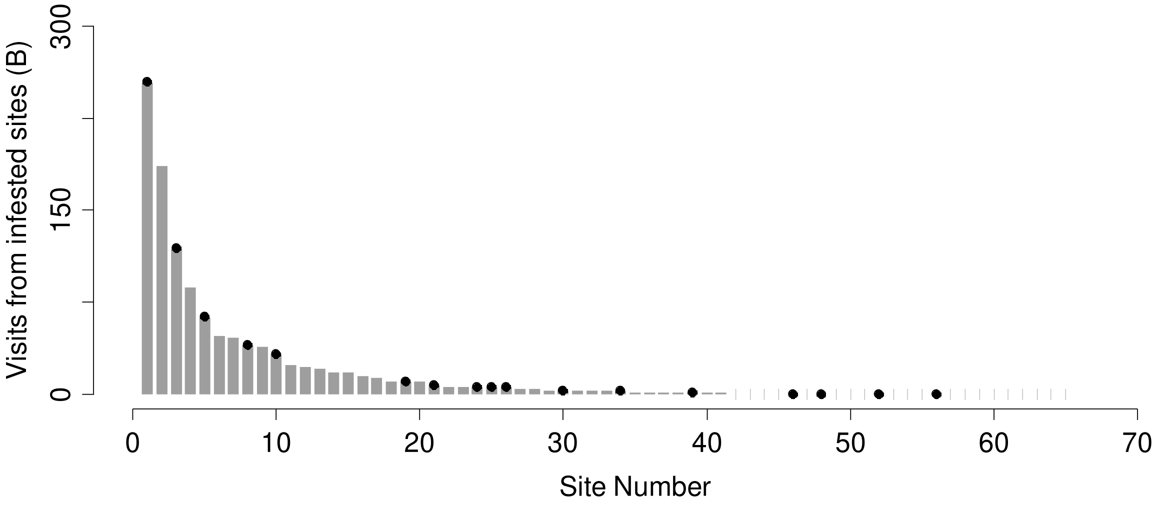

Figure 2. Invasion probability as a function of propagule pressure as represented by boater visitation from sites infested with *M. spicatum* in Lake Tahoe. Black circles indicate *M. spicatum* presence in 2012.