

# Predicting drivers of nuisance macrophyte cover in a regulated California stream using boosted regression tree models

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## ABSTRACT

The tremendous cost and difficulty of controlling submersed macrophyte proliferation in regulated waters drives a need for ecologically based strategies to reduce problematic macrophyte growth in the long term. Our study investigated the extent and causes of excessive submersed macrophyte growth in the Interdam Reach of Putah Creek in central California, USA, where plant biomass and propagules clog canal infrastructure downstream. In summer to fall 2011, we surveyed submersed macrophyte cover and environmental factors, including canopy cover, water velocity, depth, sediment nutrients, and substrate texture. Eurasian watermilfoil (*Myriophyllum spicatum* L.) and western waterweed [*Elodea nuttallii* (Planch.) St. John] were the most abundant species, and along with five additional species comprised our response variable of *nuisance macrophyte cover*. Using boosted regression tree models, we identified the abiotic factors most important in predicting nuisance macrophyte cover as those associated with light availability (sun hours and water depth) and flow (water velocity and substrate texture). This machine learning-based modeling approach enabled us to find biologically relevant thresholds in predicted macrophyte cover that would have been difficult or impossible to identify with standard linear models. Overall, increasing canopy shading or water depth beyond threshold values and increasing water velocity to flush out fine sediments (e.g., channel narrowing) are likely to be most effective in sustainably reducing nuisance macrophyte abundance in the Interdam Reach. Because of the cosmopolitan distributions of the most abundant species found in this study, our findings have broader relevance to water managers dealing with problem aquatic vegetation in many other regions.

*Key words:* abiotic factors, aquatic weeds, Lake Solano, machine learning models, Putah Creek, submersed macrophytes.

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## INTRODUCTION

Submersed macrophytes are natural components of many lakes and streams, and they contribute to the ecological health and productivity of aquatic ecosystems. However, overabundance of submersed macrophytes impairs ecosystem functioning and municipal, commercial, and recreational activities (Anderson 2011). When submersed macrophytes overproliferate in a regulated waterway, water resource managers face the difficult challenge of reducing macrophyte biomass. Traditional methods of submersed macrophyte control include mechanical removal and herbicide use, both of which can cause collateral damage to nontarget organisms (Nichols 1991). In addition, these methods generally have only short-term effects, thus requiring repeated and costly intervention (Anderson 2011). To control submersed macrophyte growth in a sustainable and cost-effective way, it is important to better understand how the manipulation of physical or chemical conditions of aquatic systems could reduce proliferation of submersed macrophytes in the long term.

The goal of this study was to inform sustainable management of nuisance aquatic vegetation in a regulated section of Putah Creek, called the Interdam Reach, in California, USA. Our objectives were to 1) document the extent of vegetation growth in the Interdam Reach, 2) identify the most important environmental factors driving that growth, and 3) model how macrophyte cover is predicted to vary over a range of these factors. To identify important patterns and thresholds, we modeled our data using boosted regression trees (BRTs), a relatively new modeling technique that combines classification and regression trees and machine learning to achieve high predictive accuracy (Elith et al. 2008).

## MATERIALS AND METHODS

### Site description

Putah Creek flows from the California Coast Range to the Yolo Bypass (Sacramento River floodplain) near Sacramento, CA. In the 1950s, the U.S. Bureau of Reclamation began the Solano Project to store and deliver water from Putah Creek to municipal, industrial, and agricultural users in the Sacramento Valley. Construction of the Monticello Dam in 1957 created the Lake Berryessa reservoir, which provides up to 1.93 billion m<sup>3</sup> of water storage (Harrison et al. 2001); 11 km downstream, construction of the Putah Creek

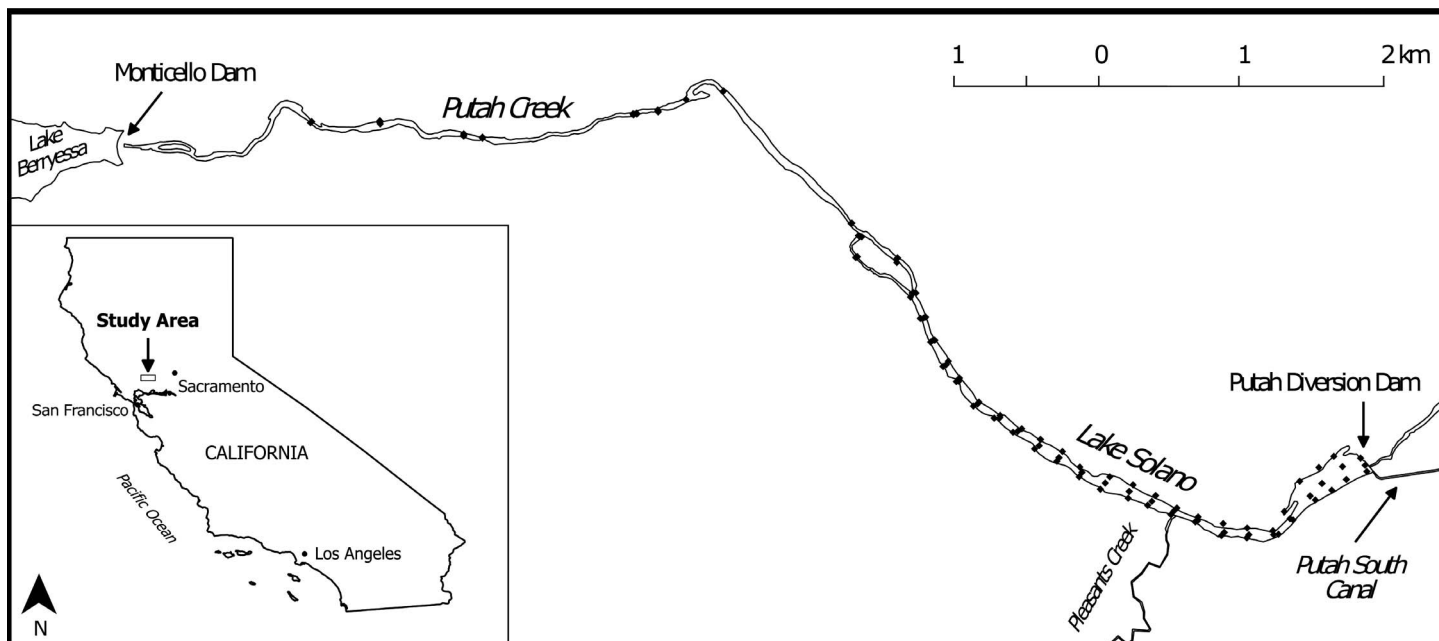


Figure 1. Map of the Putah Creek Interdam Reach. Sampling points are marked with black diamonds; 103 points were sampled on 37 transects in 2011. Inset map shows location of study system within California.

Diversion Dam formed the Lake Solano reservoir, which stores 888,000 m<sup>3</sup> of water (Harrison et al. 2001). From the Diversion Dam, most water is diverted south through the Putah South Canal. The subject of this study, the Interdam Reach (IDR), consists of the 6.6 km of stream habitat (Putah Creek) and 4 km of slow-moving lacustrine habitat (Lake Solano) between the Monticello and Putah Diversion dams (Figure 1).

The two dams have altered the IDR flow regime: instead of seasonal flooding in the winter, flows are typically highest in the summer when water is released through the IDR to the Putah South Canal for irrigation. Decreased flood frequency and intensity in the IDR have caused sediment to accumulate, particularly in the wide, shallow section of Lake Solano, just upstream of the Putah Diversion Dam. Submersed macrophytes are abundant in this reach. Throughout the summer, tens of thousands of macrophyte fragments flow into the Putah South Canal Headworks each hour, clogging intake screens and infrastructure within the canal (Northwest Hydraulic Consultants 2010). Seeds and vegetative propagules establish and grow inside the canal itself, and their decay impairs drinking water quality. As a result, canal clean-outs must be conducted every year. Finding long-term solutions for reducing macrophyte biomass in the IDR by manipulating environmental factors could reduce vegetation management costs and improve ecosystem functioning.

### Sampling methods

The two sections of the IDR were sampled in two stages: Lake Solano, the deeper 4.0-km stretch of the IDR directly upstream of the Putah Diversion Dam, was surveyed by canoe from 23 to 26 August 2011; the 6.6-km stretch of

Putah Creek between Lake Solano and the Monticello Dam was surveyed by foot on 12 to 21 November 2011. Repeat surveys in Lake Solano in November 2011 showed very similar percentage of macrophyte coverage in August and November (Peffer 2013); therefore, we did not expect the difference in sampling times to significantly affect our results.

In Lake Solano, 24 transects were established across the channel at 175-m intervals. In Putah Creek, 13 transects across the channel were established, with locations based on accessibility and the intention to sample physically variable habitats. Three points were sampled (when possible) on each transect, located 1 m inward from the each bank and in the middle of the channel (Figure 1). In total, we sampled 72 points from Lake Solano and 31 points from Putah Creek.

At each sampling point, we measured the following: percentage of cover by all macrophyte species found in a 0.25-m<sup>2</sup> quadrat; qualitative estimate of substrate size class using a modified Wentworth scale (Wentworth 1922) (Table 1); water velocity at 10 cm depth with a Student Stream Flowmeter<sup>1</sup>; and water depth. In addition, we measured the amount of canopy shading at each sampling point with a Solar Pathfinder.<sup>2</sup> Using the measure of canopy shading and the coordinates of the sampling points, we calculated *sun hours*—the average daily solar radiation reaching a location

TABLE 1. SIZE CLASSES OF SUBSTRATES USED IN A SUBSTRATE QUALITATIVE ASSESSMENT SCALE FOR THIS STUDY.

Substrate Type	Size Distribution (mm)
Soft substrate (silt/clay)	< 1/16
Sand	1/16–1
Gravel	1–64
Rock	64–256
Boulders	> 256

over 1 yr ( $\text{kWh m}^{-2} \text{d}^{-1}$ )—with Solar Pathfinder Assistant PV Software.<sup>2</sup>

We took sediment cores (when possible) measuring 5 cm in diameter and  $\sim 15$  cm deep at one randomly selected point on each transect using an AMS Multi-stage sludge and sediment sampler.<sup>3</sup> We analyzed sediment samples for nitrate, ammonium (KCl extraction), and plant-available inorganic phosphorus (Olsen-P method; Murphy and Riley 1962). The University of California, Davis Analytical Laboratory in Davis, CA (<http://anlab.ucdavis.edu>), analyzed sediment total nitrogen and carbon (SOP 320; AOAC 1997) and particle size distribution (SOP 470; Sheldrick and Wang 1993).

To characterize general water nutrient levels and clarity during the study (not for use in the models), we took water samples near the downstream, middle, and upstream portions of Lake Solano and in two locations in Putah Creek. These were analyzed for nitrate and ammonium (SOP 847; American Public Health Association 1998a,b; Knepel 2003) and orthophosphate (SOP 865.03; American Public Health Association 1998c) by the University of California, Davis Analytical Laboratory. We also measured photosynthetically active radiation (PAR) at 0.5-m intervals from the surface of the water to the bottom in the middle point of each transect with a LI-COR LI-193 spherical quantum sensor<sup>4</sup> to calculate vertical extinction coefficients,  $k_d$  ( $k_d = [\ln I_o - \ln I_z]/z$ , where  $I_o$  is the light intensity just below the water's surface, and  $I_z$  is the light intensity at depth  $z$ ).

## Modeling approach

To explore the relationships between measured environmental factors and macrophyte abundance in the IDR, we created BRT models using R software (R version 2.15.2, R Development Core Team, Vienna, Austria) with the *gbm* package version 1.6 (Ridgeway 2013). In BRT modeling, multiple decision trees, also called *classification and regression trees* (CART), are combined into models with high predictive accuracy using machine-learning algorithms. The basic CART method involves iteratively splitting the data into binary partitions based on a single explanatory variable (e.g., macrophyte cover). Each split maximizes the homogeneity of the partitions, with the resulting model explaining the maximum amount of variation in the overall data set (for a statistical overview, see Breiman et al. 1984). Some advantages of trees include their ability to model high-order interactions, to incorporate any type of predictor variables, and to handle missing data. Furthermore, trees do not assume linear relationships between variables, rarely select irrelevant predictors, and are insensitive to outliers (De'ath and Fabricius 2000; Elith et al. 2008). However, trees typically have low predictive ability and can be difficult to interpret. The BRT method builds on the strengths of CART by using boosting to improve predictive performance and interpretability (De'ath 2007). In BRT modeling, *boosting* refers to the process of creating many simple trees in succession, with each tree built on the residual error of the previous tree. The trees are then combined into a single predictive model. The number of trees that comprise a

model and the *shrinkage*—the weight put on the previous tree's residual error at each iterative model fitting step—can be optimized using cross-validation (Elith et al. 2008). Multiple BRT models can be created, and averaging their predictions leads to improved performance over a single BRT model (De'ath 2007). This ensemble method differs from traditional methods, which typically fit only one “best” model from the data.

We chose BRT to model our data because of the method's high predictive performance and because, compared with traditional linear models, BRT is better able to identify nonlinearities like threshold effects, which are common in ecological data and important for management. In addition, BRT commonly outperforms other complex, computationally demanding methods (Leathwick et al. 2006, De'ath 2007). Elith et al. (2008) and De'ath (2007) provide thorough overviews of this technique, including underlying theory, comparisons to other statistical methods, visualization of results, and examples using ecological data. To our knowledge, this is the first example of BRT being used to model macrophyte abundance; however, boosted regression trees have been used for a variety of research questions, including identifying determinants of marine fish richness (Leathwick et al. 2006) and terrestrial plant diversity (Thuiller et al. 2006), understanding effects of climate change on bird distributions (Triviño et al. 2011), and determining the roles of climate and human activity on the spread of an invasive insect (Roura-Pascual et al. 2011).

We created 150 BRT models from bootstrapped samples of the full data set. We resampled by transect, rather than by individual points, to reduce fitting based on spatial autocorrelation. As decided by the .632 bootstrap procedure (Efron 1983), each model was based on 4,100 trees, with each tree having two splits (three branches), and a shrinkage value of 0.001. Each model was generated using approximately 63.2% of the data, allowing us to test the ability of each model to predict the remaining (out-of-sample) data.

Predictor variables used in the models are presented in Table 2 with summary statistics. All but three predictors were continuous variables. *System* (Lake Solano or Putah Creek) and *Position* (left, middle, or right sampling location on a transect when facing upstream) were categorical. Qualitatively assessed substrate was also treated as a categorical variable. Because some sampling points had more than one substrate class present, this variable was input as the proportion of a given substrate class at each sampling point, divided evenly among the number of substrate types present. For example, if a point had both classes 1 and 4, the substrate for that point was assigned as 50% substrate 1 and 50% substrate 4.

For our response variable of total nuisance macrophyte abundance, we combined the percentage of cover for the following submersed macrophyte species: eurasian watermilfoil (*Myriophyllum spicatum* L.), leafy pondweed (*Potamogeton foliosus* Raf.), sago pondweed [*Stuckenia pectinata* (L.) Börner], horned pondweed (*Zannichellia palustris* L.), western elodea [*Elodea nuttallii* (Planch.) St. John], curly pondweed (*Potamogeton crispus* L.), and coontail (*Ceratophyllum demersum* L.). These species made up most ( $\sim 95\%$ ) of the submersed macrophyte cover in the IDR and are the most problematic,

TABLE 2. SUMMARY STATISTICS FOR PREDICTOR VARIABLES.

Predictor Variable	Variable Type	Average <sup>1</sup>	Standard Deviation	Range	No.
Water velocity (m s <sup>-1</sup> )	Continuous	0.17	0.22	0.05–1.81	103
Depth (m)	Continuous	1.04	0.74	0.15–3.80	103
Sun hours-yearly (kWh m <sup>-2</sup> d <sup>-1</sup> )	Continuous	3.58	1.27	0.95–4.87	102
Sand (%)	Continuous	58	23	15–88	24
Silt (%)	Continuous	28	18	5–64	24
Clay (%)	Continuous	15	6	6–30	24
Sediment N (total %)	Continuous	0.097	0.064	0.023–0.347	26
Sediment C (total %)	Continuous	1.13	0.64	0.21–3.50	26
Sediment nitrate (µg g <sup>-1</sup> )	Continuous	0.15	0.15	0.07–0.80	26
Sediment ammonium (µg g <sup>-1</sup> )	Continuous	37.4	42.9	0.9–191	26
Sediment soluble P (µg g <sup>-1</sup> )	Continuous	6.8	3.12	1.4–15.5	23
Substrate (qualitative scale)	Ordinal	1	—	1–5	87
Position	Categorical	—	—	Right, middle, left	103
System	Categorical	—	—	Lake Solano, Putah Creek	103

<sup>1</sup>Averages are arithmetic means, except for “substrate,” which is the modal value.

either because of their extensive growth within the Putah South Canal (first four species listed) or because they produce a significant amount of floating plant material that can clog screens at the canal Headworks (all seven species listed), as determined by a prior vegetation monitoring study and personal observations (Northwest Hydraulic Consultants 2010, Peffer 2013). Mosses were excluded from the calculation of total nuisance macrophyte cover because, even though moss cover was often high on boulders, mosses do not produce large quantities of biomass. The response variable for the percentage of cover was converted to a discrete variable composed of 20 “spaces” per sampling point and was modeled as a binomial process, whereby each space could be either occupied or not occupied by nuisance macrophytes.

Using the BRT model results, we calculated relative importance of each variable in predicting nuisance macrophyte cover with the *summary* function in the *gbm* package. The relative importance of a variable describes the percentage by which a model improves over a baseline model by adding that variable. To quantify relative importance, the number of times a predictor variable is chosen for splitting the data is summed, and that number is weighted by the squared improvement to each model resulting from each split. These values are averaged over all trees, and the relative importance of all predictors is scaled to sum to 100 (Elith et al. 2008). For the six top predictors, we modeled predicted macrophyte abundance across the range of values found in the data set. By averaging over all models, we obtained mean predictions, 50% confidence intervals (25 and 75% quantiles), and 95% confidence intervals (2.5 and 97.5% quantiles).

Overall model performance was assessed using the .632 bootstrap method, which provides a good estimate of out-of-sample prediction accuracy (Efron 1983). Because each of the 150 BRT models was generated using only 63.2% of the data, we could make  $R^2$  estimates of model performance using both in-sample and out-of-sample prediction estimates for each model. However, in-sample prediction tends to be overconfident, whereas out-of-sample prediction tends to be underconfident. The .632 bootstrap evaluation method creates a weighted average  $R^2$  by combining in-

sample and out-of-sample  $R^2$  estimates, weighting each by 0.368 and 0.632, respectively.

## RESULTS AND DISCUSSION

### Background conditions

The percentage of cover by nuisance submersed macrophytes was high throughout the IDR, with 68 out of 103 sampled points having 80% or greater cover (Figure 2). In both the Lake Solano and Putah Creek sections of the IDR, cover ranged from 0 to 100%.

The submersed macrophytes found in the IDR, in order of greatest to least average percentage of cover, were eurasian watermilfoil, western waterweed, curly pondweed, coon’s tail, sago pondweed, horned pondweed, bryophytes, and leafy pondweed. (Figure 3). All of these species are native to California, except eurasian watermilfoil and curly pondweed. The percentage of sampling points in which each taxon was present followed a similar pattern, but

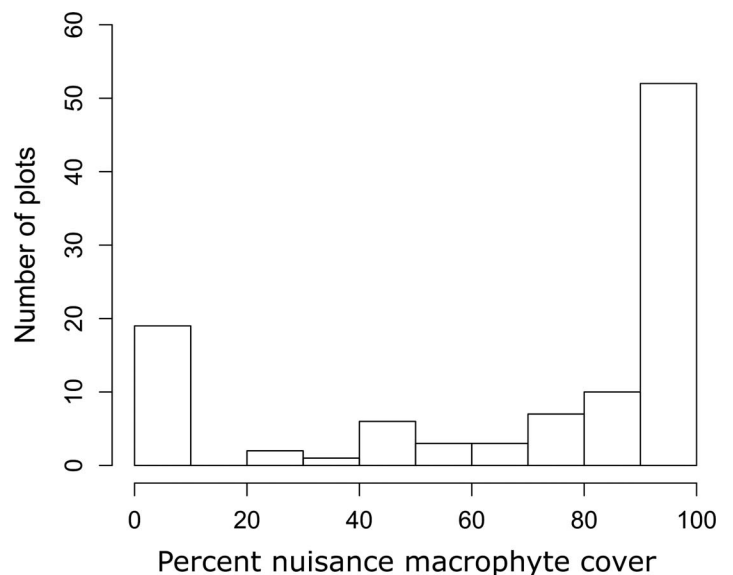


Figure 2. Histogram of the percentage of cover by nuisance submersed macrophytes in all 103 sampled plots in the Interdam Reach.

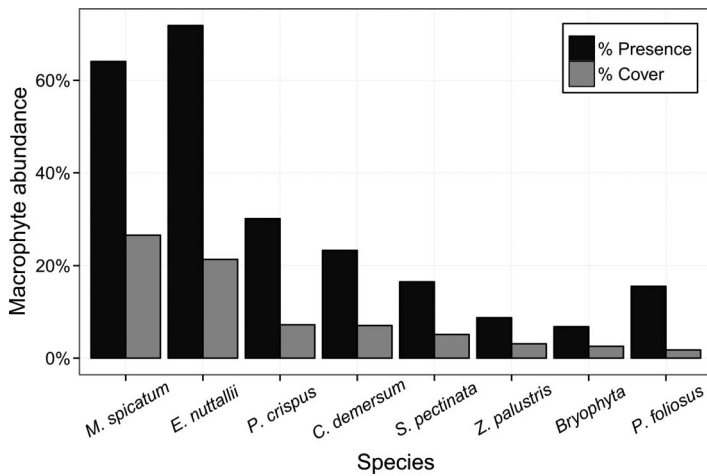


Figure 3. Occurrence of nuisance submersed macrophyte taxa throughout the Interdam Reach. Dark bars show the percentage of sampling points in which a taxon was present, and light bars show average percentage of cover across sampling points.

western waterweed was found more frequently than eurasian watermilfoil.

All water samples came back below detection limits ( $0.05 \text{ mg L}^{-1}$ ) for ammonium and soluble phosphorus. Water nitrate values were  $0.12 \text{ mg L}^{-1}$  and  $0.09 \text{ mg L}^{-1}$  at upstream and downstream transects, respectively, in Putah Creek. Water samples from the upstream and middle points in

Lake Solano both had nitrate concentrations of  $0.06 \text{ mg L}^{-1}$ , whereas the downstream sample was below detection limits.

Vertical extinction coefficients, which measure light reduction per unit depth, averaged  $0.46 \text{ m}^{-1}$  and were similar throughout the system. This value is in the low to middle range for freshwater lakes (Kirk 1994), indicating relatively clear water.

### Modeling results

Relative performance of all predictor variables used in the BRT models is presented in Figure 4, and predictions of total cover by nuisance macrophytes along the ranges of each of the six most important predictor variables are shown in Figure 5. The most important physical factors associated with nuisance submersed macrophyte growth in the BRT models were those associated with light availability (sun hours and water depth) and flow (water velocity and substrate class).

Yearly mean *sun hours*—the average daily solar radiation reaching a location over 1 yr (Figure 5A)—was the most important predictor variable for nuisance macrophyte cover in the BRT models, with 24.7% of the explanatory power. Therefore, this study joins others that have found light availability to be one of the most important predictors of macrophyte abundance in streams (e.g., Canfield and Hoyer 1988, Ali et al. 2011, Wood et al. 2012). Because negative correlations between riparian shading and sub-

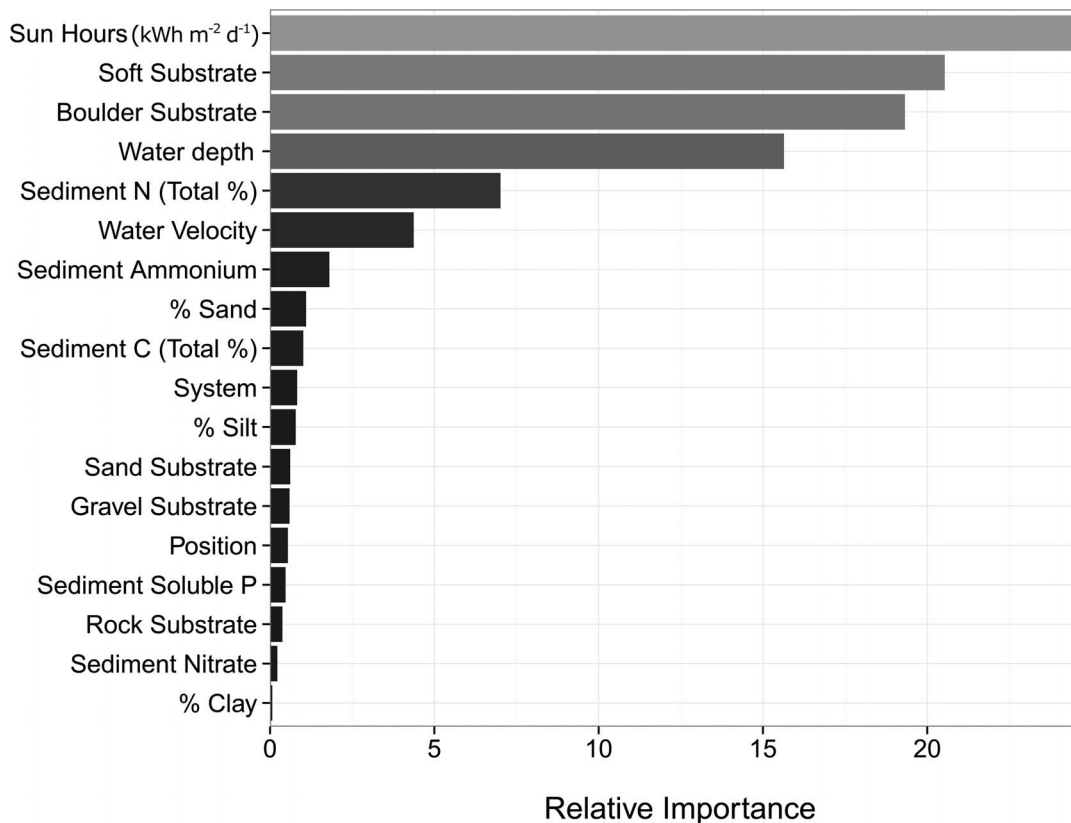


Figure 4. Relative importance of 18 variables (see Table 2) used in the boosted regression tree models for predicting nuisance macrophyte abundance. Relative importance of a variable describes the proportion of variation in the data explained by that variable relative to all other variables in the model.

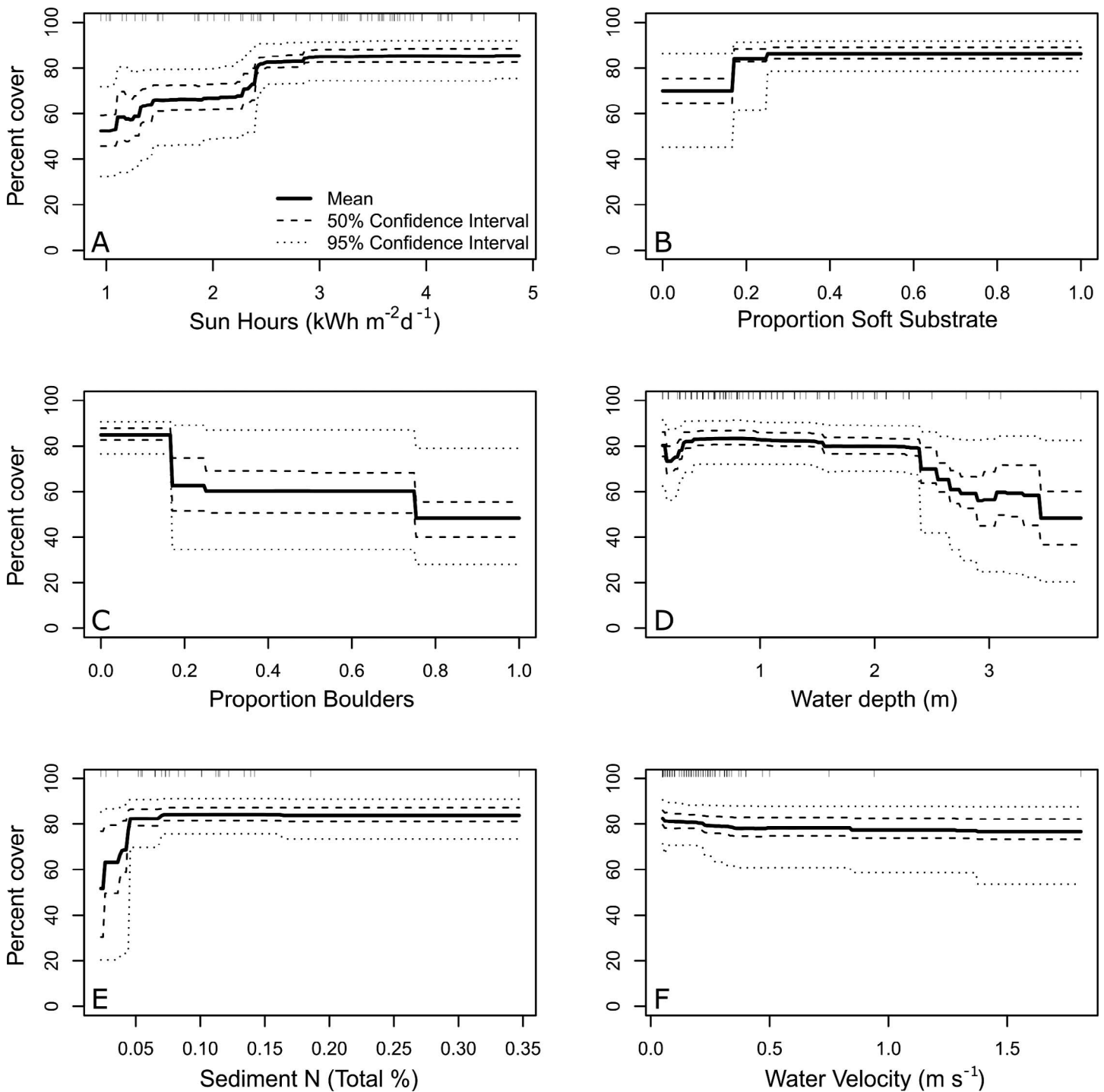


Figure 5. (A–F) Panels show predicted nuisance macrophyte percentage of cover over the range of each of the top six predictor variables. Values were generated from 150 boosted regression tree models fitted to bootstrapped samples from the original data. Means and confidence intervals came from averaging over all models; 50 and 95% confidence intervals were based on 25 and 75% quantiles and the 2.5 and 97.5% quantiles, respectively. Tick marks at the top of plots A, D, E, and F show the distribution of observed points.

mersed macrophyte abundance have been identified by numerous studies (e.g., Madsen and Adams 1989, Köhler et al. 2010, Julian et al. 2011), increasing riparian shading has been recommended as a management strategy for reducing submersed macrophyte growth (Dawson and Kern-Hansen 1979, Anderson 2011). The importance of sun hours in our

study suggests reducing incident light levels in the IDR should be prioritized. However, sun hours were positively associated with greater macrophyte cover only up to approximately  $2.4 \text{ kWh m}^{-2} \text{ d}^{-1}$ , above which greater solar radiation was predicted to have little effect on macrophyte cover (Figure 5A). At sampling points with sun hours of

approximately  $2.4 \text{ kWh m}^{-2} \text{ d}^{-1}$  and higher, macrophyte cover was predicted to be around 80%. Below this, macrophyte cover was predicted to be around 65% or less. A value of  $2.4 \text{ kWh m}^{-2} \text{ d}^{-1}$  corresponds to approximately 50% canopy cover, although orientation of canopy cover influences this calculation. Thus, increasing riparian shading in this system could be effective in reducing macrophyte abundance but only in areas where achieving high levels of canopy cover are possible.

Another factor associated with light availability in this relatively shallow, clear system is water depth, and this was the fourth most important factor in the BRT models with a relative importance of 15.6%. Depths between 0.3 and 2.4 m showed relatively little difference in predicted macrophyte cover (Figure 5D). A small reduction in macrophyte cover was predicted at the shallowest depths, which may be due to yearly water level fluctuations that cause shallow depths to dry out at certain times of the year. However, in general, nuisance submersed macrophyte cover was predicted to decrease with increasing depth, but only at depths exceeding 2.4 m. The similar predicted macrophyte cover over a range of shallow depths suggests that, as with sun hours, light is probably only limiting macrophyte growth below a threshold level. Given a typical amount of light at the surface of unshaded water in the summer in central California ( $\sim 1,900 \mu\text{mol m}^{-2} \text{ s}^{-1}$  PAR) and the average vertical extinction coefficient of  $0.46 \text{ m}^{-1}$  for the IDR, a depth of 2.4 m corresponds to around  $625 \mu\text{mol m}^{-2} \text{ s}^{-1}$  PAR. This value is within the range of typical light saturation points for submersed macrophytes (Van et al. 1976, Kirk 1994). Therefore, at depths less than 2.4 m, plants may be receiving sufficient PAR, and dredging to increase water depth may reduce the growth of problem macrophytes through light limitation.

Factors associated with flow (water velocity and substrate texture) were also important predictors in the BRT models. Water velocity itself had a relative importance of 4%, and BRT model predictions show a slight negative correlation with macrophyte cover (Figure 5F). At the time of sampling, 80% of points had water velocities of  $0.25 \text{ m s}^{-1}$  or less, with 41% being below detection limits, indicating relatively low water velocities throughout the IDR. Because the water velocity data used in the BRT models were collected at single time points, they do not reflect the full range of velocities that occur intra-annually and interannually. However, they do represent an approximation of *relative* water velocities across sampling points within the IDR.

Previous studies have found complicated, and sometimes contradictory, effects of water velocity on submersed macrophyte growth (reviewed in Madsen et al. 2001). At lower ranges, increasing water velocity may enhance growth rates by increasing gas and nutrient exchange (Westlake 1967, Madsen and Sondergaard 1983); however, high water velocity can remove fine sediments that are favorable for macrophyte growth and physically remove, damage, or stress macrophytes and their propagules (Madsen et al. 1993, Riis and Biggs 2003).

In this study, substrate class was a better indicator of flow rates over the long term than water-velocity measurements because faster flows remove fine sediments and leave

coarser materials behind over time, whereas slower flows allow sediments to settle out. The finest and coarsest substrates (soft substrate and boulders) were found to be the second and third most important factors in the BRT models with 20.5 and 19.3% of the importance, respectively. Soft substrate was positively correlated with nuisance macrophyte cover (Figure 5B), whereas boulders were negatively correlated (Figure 5C). Most sampling points (62%) contained soft substrate, whereas only 17% had boulders.

Of course, in addition to being an indicator of water flow, substrate class itself is important to macrophyte abundance because larger classes (rocks and boulders) provide a less-hospitable rooting medium (Sculthorpe 1967). Interestingly, although sediment texture has been shown to influence growth rates of submersed macrophytes (Barko and Smart 1986), the quantitative measures of particle-size distribution in the sediment (percentage of sand, silt, and clay) were not important predictors in the BRT models.

The accumulation of fine sediments in the IDR may be caused, at least in part, by the moderation of flows between the Monticello and Putah Diversion dams. Periodic high-flow events are known to reduce macrophyte proliferation (Lacoul and Freedman 2006), and planned “flushing flows” to remove sediments and vegetation have been used successfully to control macrophytes in flow-regulated rivers (Rorslett and Johansen 1996, Merz and Setka 2004, Batalla and Vericat 2009). Such planned dam releases may be a viable solution for reducing nuisance macrophyte growth in the IDR as well, although downstream effects are important to consider.

Whether sediment nutrients have an important role in controlling submersed macrophyte abundance is controversial. Sediment fertilization in experimental conditions often results in increased growth of submersed macrophytes (e.g., Best et al. 1996; Carr and Chambers 1998). However, when background nutrient levels are high in situ, other factors, such as light and carbon dioxide availability, often trump the importance of nutrients in limiting macrophyte growth, and it may only be in oligotrophic systems that sediment nutrients have an influential role in macrophyte abundance (Barko et al. 1991, Carr et al. 1997). Of the sediment nutrients measured in this study—nitrate, ammonium, total N, total C, and soluble P—only sediment total N was an important predictor of nuisance submersed macrophyte growth (7.0% relative importance). However, a reduction in cover was only predicted to occur below 0.05% (Figure 5E), and only three sampling points of 26 were at or below 0.05% N. Because our models are based on correlations, we cannot distinguish whether low sediment N causes lower macrophyte growth or whether decreased macrophyte growth causes less accumulation of sediment N. However, one might expect that if the latter were true, a linear relationship would be detected, instead of the more asymptotic relationship that was predicted in the BRT models.

The relative importance of the remaining predictors was less than 2%. Notably, *system* was among these less-important predictors, indicating that sampling differences

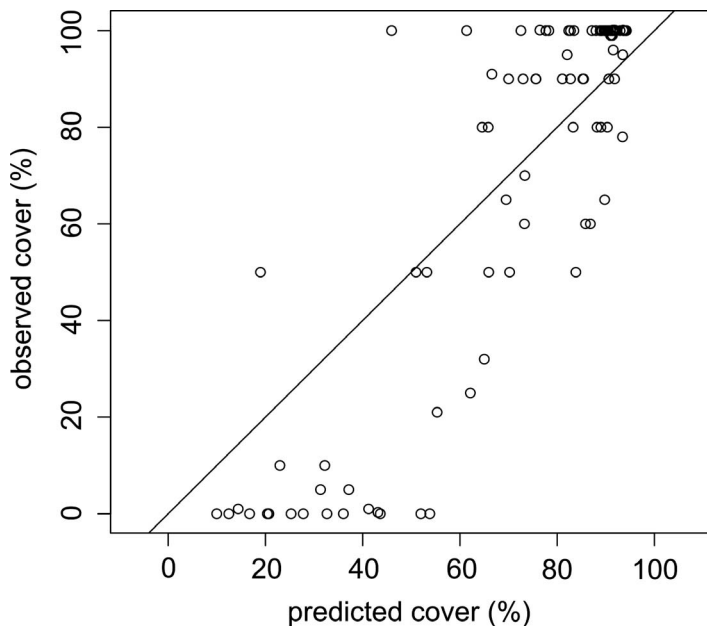


Figure 6. Plot of average model predictions of the nuisance macrophyte percentage of cover at a sampling point versus observed values from field-collected data. Line shows an ideal 1:1 relationship between predicted and observed values. The models tend to predict values that are less extreme than the observed values.

between the Lake Solano and Putah Creek sections of the IDR did not strongly affect model predictions.

Evaluation of model performance using the .632 bootstrap method yielded an  $R^2$  of 0.60. The models tended to underpredict high values and overpredict low values, as seen in Figure 6. This occurs for two main reasons: first, with binomial data, predicting extremes often results in overfitting, and it's "safer" to predict intermediate values; second, averaging over 150 predictions smooths out more extreme predictions that might arise in only a subset of models.

### Management implications and conclusions

Overall, we found a high abundance of nuisance submersed macrophytes in the IDR, which can be attributed largely to the high percentage of shallow, unshaded aquatic habitat, with low to moderate water velocity and fine sediments. Perhaps the best solution for addressing these factors would be narrowing and deepening the main channel of the IDR, particularly in Lake Solano and planting canopy-forming vegetation along the banks. This would decrease light availability, increase water velocity (thus decreasing fine sediments), and also decrease the total amount of available habitat for submersed macrophytes. Increased shading and faster transport of water through the IDR, which comes from the hypolimnetic discharge from the Monticello Dam, would also decrease water temperatures. Although not modeled in this study, lower water temperatures are associated with reduced macrophyte growth rates and reproduction (Barko and Smart 1981, Barko et al. 1982, Lacoul and Freedman 2006). Therefore, channel modification, although resource-intensive in the

short term, may be the most sustainable approach to reducing problematic macrophyte growth in the IDR.

Identifying and understanding the primary drivers of nuisance macrophyte abundance is important for prioritizing management actions in regulated streams and constructed waterways. Using BRT as a modeling approach resulted in a high level of in-sample predictive accuracy ( $R^2 = 0.60$ ) and enabled us to find important, biologically meaningful thresholds in our predictor variables, which might not have been discovered by more traditional linear-modeling approaches. Because the most abundant submersed macrophyte species identified in this study were cosmopolitan in distribution, our findings have relevance to managers grappling with macrophyte overabundance worldwide. To our knowledge, our study represents the first use of BRT in identifying and modeling the most important factors predicting submersed macrophyte cover. A similar approach could be useful for managers of many types of wetland and aquatic systems looking to understand and apply limited resources to a variety of nuisance taxa.

### SOURCES OF MATERIALS

<sup>1</sup>GEOPACKS, Unit 4A, Hatherleigh Industrial Estate, Holsworthy Road, Hatherleigh, Devon EX20 3LP, England.

<sup>2</sup>Solar Pathfinder, 3953 Marsh Creek Road, Linden, TN, 37096.

<sup>3</sup>AMS, Inc., 105 Harrison Street, American Falls, ID 83211.

<sup>4</sup>LI-COR, 4647 Superior Street, P.O. Box 4425, Lincoln, NE 68504.

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### LITERATURE CITED

- Ali MM, Hassan SA, Shaheen ASM. 2011. Impact of riparian trees shade on aquatic plant abundance in conservation islands. *Acta Bot. Croat.* 70:245–258.
- American Public Health Association. 1998a. Method 4500-NH<sub>3</sub> H, flow injection analysis (proposed), pp. 4-111–4-112. In: L. S. Clesceri, A. E. Greenberg, A. D. Eaton (eds.). *Standard methods for the examination of water and wastewater*. 20th ed. APHA, Washington, DC.
- American Public Health Association. 1998b. Method 4500-NO<sub>3</sub> I, cadmium reduction flow injection method (proposed), pp. 4-121–4-122. In: L. S. Clesceri, A. E. Greenberg, A. D. Eaton (eds.). *Standard methods for the examination of water and wastewater*. 20th ed. APHA, Washington, DC.
- American Public Health Association. 1998c. Method 4500-P G, flow injection analysis for orthophosphate, pp. 4-149–4-150. In: L. S. Clesceri, A. E. Greenberg, A. D. Eaton (eds.). *Standard methods for the examination of water and wastewater*. 20th ed. APHA, Washington, DC.
- Anderson L. 2011. Freshwater plants and seaweeds, pp. 248–258. In: D. Simberloff, M. Rejmanek (eds.). *Encyclopedia of biological invasions*. University of California Press, Berkeley, CA.
- AOAC. 1997. AOAC official method 972.43, microchemical determination of carbon, hydrogen, and nitrogen, automated method, Chapter 12, pp. 5–6. In: *Official methods of analysis of AOAC International*. 16th ed. AOAC International, Arlington, VA.
- Barko JW, Gunnison D, Carpenter SR. 1991. Sediment interactions with submersed macrophyte growth and community dynamics. *Aquat. Bot.* 41:41–65.



- Barko JW, Hardin DG, Matthews MS. 1982. Growth and morphology of submersed freshwater macrophytes in relation to light and temperature. *Can. J. Bot.* 60:877–887.
- Barko JW, Smart RM. 1981. Comparative influences of light and temperature on the growth and metabolism of selected submersed fresh-water macrophytes. *Ecol. Monogr.* 51:219–235.
- Barko JW, Smart RM. 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. *Ecology* 67:1328–1340.
- Batalla RJ, Vericat D. 2009. Hydrological and sediment transport dynamics of flushing flows: Implications for management in large Mediterranean rivers. *River Res. Appl.* 25:297–314.
- Best EPH, Woltman H, Jacobs FHH. 1996. Sediment-related growth limitation of *Elodea nuttallii* as indicated by a fertilization experiment. *Freshw. Biol.* 36:33–44.
- Breiman L, Friedman J, Olshen R, Stone C. 1984. Classification and regression trees. Wadsworth International Group, Belmont, CA.
- Canfield DE, Hoyer MV. 1988. Influence of nutrient enrichment and light availability on the abundance of aquatic macrophytes in Florida streams. *Can. J. Fish. Aquat. Sci.* 45:1467–1472.
- Carr GM, Chambers PA. 1998. Macrophyte growth and sediment phosphorus and nitrogen in a Canadian prairie river. *Freshw. Biol.* 39:525–536.
- Carr GM, Duthie HC, Taylor WD. 1997. Models of aquatic plant productivity: A review of the factors that influence growth. *Aquat. Bot.* 59:195–215.
- Dawson FH, Kern-Hansen U. 1979. The effect of natural and artificial shade on the macrophytes of lowland streams and the use of shade as a management technique. *Int. Rev. Gesamt. Hydrobiol.* 64:437–455.
- De'ath G. 2007. Boosted trees for ecological modeling and prediction. *Ecology* 88:243–251.
- De'ath G, Fabricius KE. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology*. 81:3178–3192.
- Efron B. 1983. Estimating the error rate of a prediction rule: Improvement on cross-validation. *J. Am. Statist. Assoc.* 78:316–331.
- Elith J, Leathwick JR, Hastie T. 2008. A working guide to boosted regression trees. *J. Anim. Ecol.* 77:802–13.
- Harrison LL, MacArthur RC, Sanford RA. 2001. Lake Solano sediment management study. *Watershed Manage. Oper. Manage.* 2000:1–10.
- Julian JP, Seegert SZ, Powers SM, Stanley EH, Doyle MW. 2011. Light as a first-order control on ecosystem structure in a temperate stream. *Ecohydrology* 4:422–432.
- Kirk JTO. 1994. Light and photosynthesis in aquatic ecosystems. 2nd ed. Cambridge University Press, Cambridge, UK.
- Köhler J, Hachol J, Hilt S. 2010. Regulation of submersed macrophyte biomass in a temperate lowland river: Interactions between shading by bank vegetation, epiphyton and water turbidity. *Aquat. Bot.* 92:129–136.
- Knepel, K. 2003. Determination of nitrate in 2M KCl soil extracts by flow injection analysis. QuikChem method 12-107-04-1-B. Lachat Instruments, Loveland, CO.
- Lacoul P, Freedman B. 2006. Environmental influences on aquatic plants in freshwater ecosystems. *Environ. Rev.* 14:89–136.
- Leathwick JR, Elith J, Francis MP, Hastie T, Taylor P. 2006. Variation in demersal fish species richness in the oceans surrounding New Zealand: An analysis using boosted regression trees. *Mar. Ecol. Prog. Ser.* 321:267–281.
- Madsen JD, Adams MS. 1989. The distribution of submerged aquatic macrophyte biomass in a eutrophic stream, Badfish Creek: The effect of environment. *Hydrobiologia* 171:111–119.
- Madsen JD, Chambers PA, James WF, Koch EW, Westlake DF. 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia* 444:71–84.
- Madsen TV, Enevoldsen HO, Jorgensen TB. 1993. Effects of water velocity on photosynthesis and dark respiration in submerged stream macrophytes. *Plant Cell Environ.* 16:317–322.
- Madsen TV, Sondergaard M. 1983. The effects of current velocity on the photosynthesis of *Callitriche stagnalis* Scop. *Aquat. Bot.* 15:187–193.
- Merz JE, Setka JD. 2004. Evaluation of a spawning habitat enhancement site for Chinook salmon in a regulated California River. *N. Am. J. Fish. Manage.* 24:397–407.
- Murphy J, Riley JP. 1962. A modified single-solution method for the determination of phosphate in natural waters. *Anal. Chem. Acta* 27:31–36.
- Nichols SA. 1991. The interaction between biology and the management of aquatic macrophytes. *Aquat. Bot.* 41:225–252.
- Northwest Hydraulic Consultants. 2010. Species identification and seasonal biomass flux monitoring in Putah South Canal, September 2008 through September 2009. Northwest Hydraulic Consultants, Sacramento, CA.
- Peffer E. 2013. Aquatic vegetation assessment of Putah Creek, Lake Solano, the Putah South Canal, and the Terminal Reservoir July 2011–June 2013. Solano County Water Agency, Vacaville, CA.
- Ridgeway G. 2013. gbm: Generalized Boosted Regression Models. R package version 1.6. <http://CRAN.R-project.org/package=gbm>. Accessed June 10, 2013.
- Riis T, Biggs BJF. 2003. Hydrologic and hydraulic control of macrophyte establishment and performance in streams. *Limnol. Oceanogr.* 48:1488–1497.
- Rorslett B, Johansen SW. 1996. Remedial measures connected with aquatic macrophytes in Norwegian regulated rivers and reservoirs. *Regul. Rivers Res. Manage.* 12:509–522.
- Roura-Pascual N, Hui C, Ikeda T, Leday G, Richardson DM, Carpintero S, Espadaler X, Gómez C, Guénard B, Hartley S, Krushelnycky P, Lester PJ, McGeoch MA, Menke SB, Pedersen JS, Pitt JPW, Reyes J, Sanders NJ, Suarez A V, Touyama Y, Ward D, Ward PS, Worner SP. 2011. Relative roles of climatic suitability and anthropogenic influence in determining the pattern of spread in a global invader. *Proc. Natl. Acad. Sci. U. S. A.* 108:220–225.
- Sheldrick BH and Wang C. 1993. Particle-size Distribution. pp. 499–511. In: Carter M. R. (ed.). Soil sampling and methods of analysis. Canadian Society of Soil Science. Lewis, Ann Arbor, MI.
- Sculthorpe CD. 1967. The biology of aquatic vascular plants. Edward Arnold, London.
- Thuiller W, Midgley GF, Rouget M, Cowling RM. 2006. Predicting patterns of plant species richness in megadiverse South Africa. *Ecography* 79:66–744.
- Triviño M, Thuiller W, Cabeza M, Hickler T, Araújo MB. 2011. The contribution of vegetation and landscape configuration for predicting environmental change impacts on Iberian birds. *PLOS ONE* 6:e29373.
- Van TK, Haller WT, Bowes G. 1976. Comparison of the photosynthetic characteristics of three submersed aquatic plants. *Plant Physiol.* 58:761–768.
- Wentworth CK. 1922. A scale of grade and class terms for clastic sediments. *J. Geol.* 30: 377–392.
- Westlake DF. 1967. Some effects of low-velocity currents on the metabolism of aquatic macrophytes. *J. Exp. Bot.* 13:187–205.
- Wood KA, Stillman RA, Clarke RT, Daunt F, O'Hare MT. 2012. Understanding plant community responses to combinations of biotic and abiotic factors in different phases of the plant growth cycle. *PLOS ONE* 7:e49824.