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The invasive aquatic plant *Egeria densa* (Brazilian waterweed) is a submersed aquatic plant that has expanded its distribution in both its native and introduced range. Because the plant grows so densely, it can become a problem for management of waterways and habitat restoration projects.



It is difficult to remove once established and mechanical and chemical controls have shown limited effectiveness. Here we analyze the distribution of *E. densa* in the Sacramento–San Joaquin Delta (the Delta) of California, USA, using environmental variables that include mean water velocity, mean water turbidity, and water column depth. We found that increasing water column depth strongly limited *E. densa* occurrence, especially when depth at mean lower low water (MLLW) exceeds 2 m. The highest probability of occurrence occurred at locations with a water column depth of –1 to 2 m at MLLW. Turbidity had a reliably negative effect on *E. densa* occurrence; as water clarity has increased in the Delta, it has likely favored the spread of the plant. Neither mean water velocity nor maximum water velocity had a reliable effect on *E. densa* probability, in spite of scientific and observational evidence that it is sensitive to flows. These results suggest potentially serious problems with restoration projects that emphasize shallow water habitat in the range favored by *E. densa*. Without some way to manage spread of the plant—through spraying, sediment loading, or gating—channels in such projects are at risk of being taken over by *E. densa*. However, these results should be interpreted in light of the fact that water outflow in water year 2008 was very low, and that *E. densa* abundance may be partially controlled by higher water flows than those considered here.

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RESEARCH

Physical Controls on the Distribution of the Submersed Aquatic Weed *Egeria densa* in the Sacramento–San Joaquin Delta and Implications for Habitat Restoration

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ABSTRACT

The invasive aquatic plant *Egeria densa* (Brazilian waterweed) is a submersed aquatic plant that has expanded its distribution in both its native and introduced range. Because the plant grows so densely, it can become a problem for management of waterways and habitat restoration projects. It is difficult to remove once established and mechanical and chemical controls have shown limited effectiveness. Here we analyze the distribution of *E. densa* in the Sacramento–San Joaquin Delta (the Delta) of California, USA, using environmental variables that include mean water velocity, mean

water turbidity, and water column depth. We found that increasing water column depth strongly limited *E. densa* occurrence, especially when depth at mean lower low water (MLLW) exceeds 2 m. The highest probability of occurrence occurred at locations with a water column depth of –1 to 2 m at MLLW. Turbidity had a reliably negative effect on *E. densa* occurrence; as water clarity has increased in the Delta, it has likely favored the spread of the plant. Neither mean water velocity nor maximum water velocity had a reliable effect on *E. densa* probability, in spite of scientific and observational evidence that it is sensitive to flows. These results suggest potentially serious problems with restoration projects that emphasize shallow water habitat in the range favored by *E. densa*. Without some way to manage spread of the plant—through spraying, sediment loading, or gating—channels in such projects are at risk of being taken over by *E. densa*. However, these results should be interpreted in light of the fact that water outflow in water year 2008 was very low, and that *E. densa* abundance may be partially controlled by higher water flows than those considered here.

KEY WORDS

submersed aquatic vegetation, invasive organisms, estuaries, turbidity, water quality, hydrodynamics, restoration

INTRODUCTION

Among the challenges facing stream and estuarine restoration is development of appropriate geomorphic and hydrodynamic conditions to favor ecosystems that support native species. Measures to improve abiotic conditions can sometimes be rendered ineffective by the secondary invasion of alien species that out-compete or prey upon desired natives. In addition, some alien species serve as ecosystem engineers that fundamentally and irreversibly change the physical and biotic habitat, creating, in effect, novel ecosystems. The invasive aquatic plant *Egeria densa* Planchon from the frog-bit family (Hydrocharitaceae) is one such invader. Native to Brazil, Uruguay and Argentina, and distributed internationally by the aquarium trade (Cook and Urmi-König 1984; Haynes 2000), *E. densa* has expanded its range so extensively that it has become a nuisance weed throughout the temperate zones of the world (Bini et al. 1999; Bini and Thomaz 2005). Among the problems it creates are waterway blockages, reservoir flow interruption, water quality alteration, native vegetation displacement, and fish habitat degradation (Anderson 1990; Yarrow et al. 2009). The plant roots in the substrate of slow-moving rivers, lakes, and estuaries, developing elongated shoots that form a thick canopy at the water surface. Dense vertical stands reduce water velocity, which increases both sediment deposition and thermal stratification (Santos et al. 2009; Yarrow et al. 2009). The resulting increases in water clarity and temperature can promote the further growth and spread of *E. densa* itself, while facilitating invasion by other alien species, particularly fishes (Grimaldo and Hymanson 1999; Brown 2003; Nobriga et al. 2005).

Egeria densa is difficult to control once established (Curt et al. 2010; Cal-IPC 2013). Attempts at bio-control have been limited, in part because of the dearth of herbivores feeding exclusively on the plant (Yarrow et al. 2009). Control using triploid grass carp (*Ctenopharyngodon idella*) has had limited success, and poses some dangers to native organisms (Bain 1993). Control using aquatic insects and fungi has been largely ineffective (Mitchell 1980; ARS 2012; Walsh et al. 2013). Chemical control is commonly used, but requires repeated applications of herbicide to be effective, and is potentially toxic to other organisms (Yarrow et al. 2009). Mechanical control

can be effective for short periods, but rapid *E. densa* growth during warm periods allows it to quickly return after mow-down. Mowing can also promote vegetative dispersal by creating plant segments that readily disperse and propagate (Oliveira et al. 2005).

The ability of *Egeria densa* to invade and alter aquatic habitats, combined with its resistance to control, contributes to the development of restoration-resistant novel ecosystems (*sensu* Hobbs et al. 2009). This is among the challenges facing restoration projects in the Sacramento–San Joaquin Delta (the Delta) (Essex Partnership 2009; Yarrow et al. 2009), where *E. densa* became established around 1946 by introductions from the aquarium trade (Anderson 1990). Concerns about the plant as an invasive weed date from the 1990s, when it rapidly expanded its local range (Jassby and Cloern 2000). As late as 1993, *E. densa* is mentioned without alarm (Lehman 1996), but by 1996 it was reported that *E. densa* stands were harboring invasive sunfish (Centrarchidae), including the piscivorous largemouth bass (*Micropterus salmoides*) (Grimaldo and Hymanson 1999). A 1999 study suggested that *E. densa* could dominate subtidal restoration habitats in the Delta (Simenstad et al. 1999).

Dense stands of *E. densa* in the Delta facilitate fish species that do well in warm, clear, slow-moving water with vertical physical structure (Nobriga et al. 2005; Ferrari et al. 2014), particularly Centrarchidae introduced from the southeastern United States that are adapted to such conditions in their native habitat. These include bluegill sunfish (*Lepomis macrochirus*), green sunfish (*L. cyanellus*), redear sunfish (*L. microlophus*), warmouth (*L. gulosus*) and largemouth bass (Brown 2003; Nobriga et al. 2005). These fishes use the stems and canopy of *E. densa* as structure upon which to carry out feeding and predation: sunfish navigate inside stands, seeking invertebrate prey; while larger bass wait at the edges, preying upon invertebrates and fish that move along the edge (Nobriga and Feyrer 2007). The sunfish are suspected to be direct and aggressive competitors of some native fishes such as Sacramento perch (*Archoplites interruptus*), which were largely extirpated from the Delta by the 1960s (Marchetti 1999; Moyle 2002); while largemouth bass may compete with and prey upon native and introduced fishes (Nobriga and Feyrer 2007; Ferrari et al. 2014).

Anecdotal evidence suggests that *E. densa* facilitates predators' ability to capture fishes, especially species that are poorly adapted to such habitat (Brown 2003). Largemouth bass are known to feed upon splittail (*Pogonichthys macrolepidotus*), Mississippi silversides (*Menidia audens*), and sunfishes (Nobriga and Feyrer 2007). Native minnows (Cyprinidae) may be particularly vulnerable under these conditions because their streamlined, fusiform shape is best adapted to take advantage of open water or water moving along an edge. This may make them vulnerable to predation by largemouth bass while being unable to capitalize on refuges within the stands of submersed aquatic vegetation (SAV) (Ferrari et al. 2014). Likewise, regions that are altered from open water to structurally complex habitat are generally undesirable to the largely pelagic delta smelt (*Hypomesus transpacificus*) and longfin smelt (*Spirinchus thaleichthys*). In fact, such habitat may make them more vulnerable to predation (Brown 2003a, 2003b).

Tidal and subtidal restoration projects in the Delta may, therefore, be impaired by the growth of *E. densa* (Brown 2003; ERP 2013). Because large-scale restoration of such habitats to benefit native fishes is planned (ICF International 2013; CNRA et al. 2014), a model is needed that can estimate the probability of *E. densa* occurrence under conditions of different water column depth, flow, and turbidity, to help evaluate the likelihood of success of restoration projects. Here, we present such a model, based on observations of *E. densa* presence and absence at locations throughout the Delta in the 2008 growing season paired with hydrodynamic and long-term monitoring data.

METHODS

Study Location

The Delta is the easternmost region of the San Francisco Estuary (estuary), and includes the confluence of the Sacramento and San Joaquin rivers. Although it is an estuarine ecosystem with historic variation in salinity, the modern Delta has been managed as a largely freshwater environment since the mid-20th century (Conomos et al. 1985). Modifications include infrastructure to support the flow of water from the Sacramento River in the north to the south side of the Delta, where it is

pumped into a system of canals for agricultural and urban use in the central and southern parts of the state (Lund et al. 2007). However, the modern Delta environment results from changes to the estuary that began over 150 years ago, when Delta reclamation efforts responded to erosional and depositional processes set in motion by the California Gold Rush of the 1850s (Thompson 1957; Lund et al. 2007; Whipple et al. 2012). These alterations created an inverted topography typical of many of the world's anthropogenically influenced estuaries. Steep dikes border agricultural islands that have subsided below sea level from decades of plowing, burning and oxidation (Thompson 1957; Mount and Twiss 2005). These subsided islands are vulnerable to dike failure (Lund et al. 2007; Suddeth et al. 2010). Once flooded, they create deep lake-like environments that can be uneconomical or impractical to reclaim, and become characterized by deep, warm, slow-moving, low-turbidity water atypical of the historic Delta (Thompson 1957; Whipple et al. 2012). *Egeria densa* can be abundant in such habitats, but it is broadly distributed from the lower reaches of the Sacramento and San Joaquin rivers to their confluence at Sherman Lake (Santos et al. 2011), the nearshore subtidal areas of Suisun Bay, and the brackish eastern interior of Suisun Marsh (Simenstad et al. 2000; Grewell et al. 2014).

Field-Collected Data: Depth and Occurrence

Presence-absence data for *E. densa* were collected by boat in June and July of 2008 during a study on the effectiveness of hyperspectral imaging to recognize submersed and floating aquatic vegetation in the Delta (Santos et al. 2011). SAV-containing sites were randomly chosen across the known range of *E. densa* in the Delta as mapped in 2007 (Hestir et al. 2008). A similar number of sites not containing SAV were also selected (Figure 1). Plants were identified and quantified by visual observation at the water surface across a 100 m² quadrat. Each site was georeferenced, and water quality data, depth, and time of collection were recorded. For the current study, we used only the presence or absence of *E. densa*, date and time, and depth. *Egeria densa* was found at 196 out of 882 sampled sites, not including sites that were immediately proximal to the *E. densa* spraying programs

of 2008, which were eliminated from the analysis (Figure 1).

To calculate the water column depth referenced to local mean lower low water (MLLW), it was necessary to correct the measured depth at time of collection for changes in tide height. A harmonic tide calculator (WTides, Thornton 2013) was used to predict tide height relative to local MLLW at multiple sites throughout the Delta. Harmonic calculations account for all variation in tide height other than small adjustments caused by meteorological conditions. Since the data were not taken during storm conditions, the harmonic estimates should provide consistent corrections. Other studies have used the same prediction software to evaluate tide heights (Baker et al. 2007; Seabra et al. 2011). Where sample stations occurred within a channel network distance of 5,000m to WTides prediction locations, depth was corrected to MLLW depth by subtracting predicted tide height at time of sample from measured water column depth in the field. Where samples were not taken adjacent to WTides sites, the two nearest WTides sites were chosen, and tide height was calculated by linearly interpolating between the two tide height values as a function of channel network distance to the sample site. The interpolated value was then subtracted from the measured water column depth to obtain corrected water column depth at MLLW. Where sample sites were not adjacent or between WTides locations, the nearest location was taken. The corrections resulted in positive measures for water column depths greater than MLLW, and negative values for depths above MLLW.

The California Department of Boating and Waterways conducted an *E. densa* eradication campaign on Franks Tract, a flooded island, using herbicides, in spring 2008 (Santos et al. 2009; Santos et al. 2011) (Figure 1). Effects of the application were noted in June as yellowing plant tips (from April through June 2008; 2013 phone and email communications from G. Newman, California Department of Boating and Waterways, to J. Durand, unreferenced, see “Notes”). Effects were noted outside of the immediate area in Rock Slough and Old River to the railroad crossing, but it is unknown whether these effects biased survey results. We chose to omit all samples taken within Franks Tract proper, while using those outside, on

the assumption that more distant samples would not have died back until well after the field surveys were completed in early July.

Water Velocity Data

In addition to depth, we used the absolute values of mean water velocity as a predictor variable because *E. densa* may be constrained physically by water motion (Kankanamge et al. 2011). Daily averages of water velocity estimates (m s^{-1}) from October 1, 2007 to June 30, 2008, were used to analyze *E. densa* presence in June–July 2008. We estimated water velocities for each georeferenced site using a validated RMA2 (Resource Management Associates, Inc.) model for Water Year 2008. RMA2 was one of the earliest multi-dimensional models applied to estuaries and remains a widely used model for Delta analysis (King et al. 1975; King and Norton 1978; King and Rachiele 1990; RMA 2008). The RMA2 grid has both one-dimensional channels, which represent a cross-sectional averaged velocity, and two-dimensional channels, which represent vertically averaged velocities. The estimates do not reflect the effects of reduced velocity by *E. densa*. Because seasonal variation in Delta flows can vary over several orders of magnitude (Kimmerer 2002), we tried to model both mean and maximum velocities as ratios or interactive factors. However, collinearity between mean and maximum velocities (with a linear correlation coefficient of 0.898) caused the model to predict poorly; eliminating maximum velocity improved the model considerably.

Turbidity Data

We retrieved turbidity measurements from 49 Delta water quality stations from the California Data Exchange Center (CDEC) (CDEC 2013), which aggregates data from sensors deployed throughout the state (Table 1). Data were retrieved as daily averages, and used to estimate mean nephelometric turbidity units (NTUs) for that sensor. The period of record varies for each sensor (from a few months to over 25 years), potentially biasing means if conditions changed over time. To check for biased estimates we mapped sensor locations with their means, and identified regional turbidity differences (Figure 2). The pattern of turbidity appears to follow a geographic

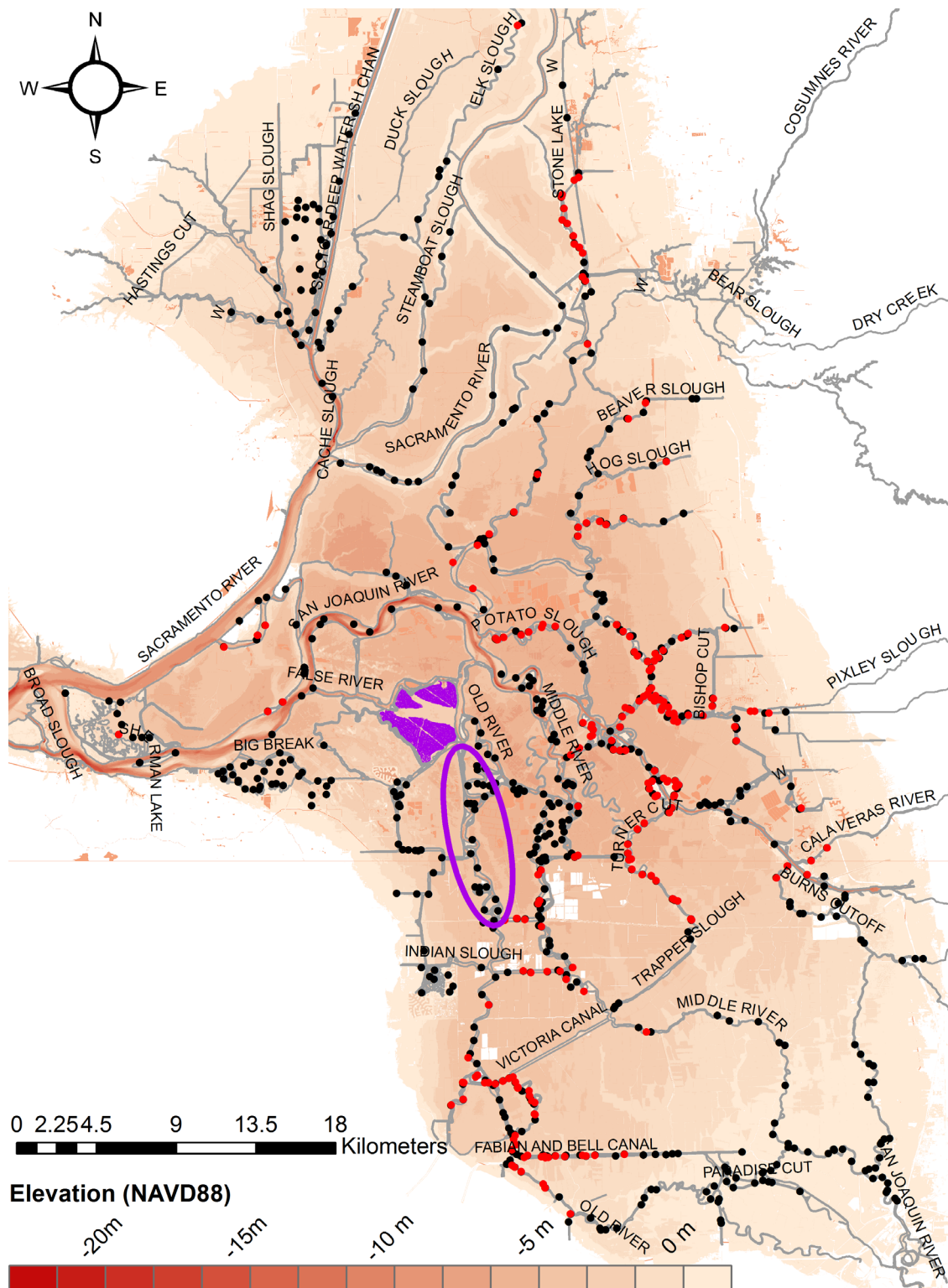


Figure 1 SAV sampling in Delta in June and July 2008. Red circles indicate *E. densa* presence; black circles indicate absence. Purple polygons show the extent of herbicide application in Franks Tract during spring 2008. Oval indicates the observed southernmost effect of herbicide application (2013 phone and email communications from G. Newman to J. Durand, unreferenced, see "Notes"). (Sources: elevation data, Wang and Ateljevich (2012); spray transect data, California Department of Boating and Waterways.)

Table 1 List of California Data Exchange Center stations used to obtain turbidity data from sites across the Delta (<http://cdec.water.ca.gov/>)

Code	Station	Longitude East	Latitude North
ANH	Antioch	121.80296	38.01783
BKS	Barker Slough	121.7965	38.2759
BLP	Blind Point	121.722	38.028
CLC	Clifton Court	121.5574	37.8298
CPP	Cordelia Pumping Plant	122.1347	38.2276
FAL	False River	121.6669	38.0558
HBP	Harvey O. Banks Pumping Plant	121.620278	37.801944
JER	Jersey Point	121.688	38.053
MDM	Middle River at Riddle River	121.534	37.943
MHO	Middle River Near Howard Road Bridge	121.383306	37.876222
OBJ	Old River at Bacon Island	121.571114	37.970001
OSJ	Old River at Franks Tract near Terminous	121.5789	38.0711
OH4	Old River at Highway 4	121.569168	37.891109
PPT	Prisoners Point	121.562	38.066
VCU	Victoria Canal Near Byron	121.5283	37.8717
MRZ	Martinez	122.138	38.028
NMR	North Mokelumne R. at W Walnut Grove Rd.	121.5071	38.2232
SMR	South Mokelumne R. at W Walnut Grove Rd.	121.4911	38.2255
RYI	Cache Slough at Ryer Island	121.6692	38.2128
DLC	Delta Cross Channel btw. Sacramento River and Snodgrass	121.505	38.245
RTM	DES Real Time Monitoring Test Station	121.567	38.587
GSS	Georgiana Slough at Sacramento River	121.518	38.237
LIB	Liberty Island at Approx Cntr S End	121.6849	38.2421
HWB	Miner Slough at Hwy 84 Bridge	121.6308	38.2917

Code	Station	Longitude East	Latitude North
DWS	Sacramento Deep Water Shipping Channel	121.66667	38.25611
SDI	Sacramento River at Decker Island	121.736	38.0934
FPT	Sacramento River at Freeport	121.5	38.45
SRH	Sacramento River at Hood	121.519	38.382
NAAL	Sacramento River at Mallard Island	121.919	38.044
SRV	Sacramento River at Rio Vista (USGS)	121.686	38.16
RVB	Sacramento River at Rio Vista Bridge	121.686355	38.159737
VON	Sacramento River at Verona	121.5982895	38.7743454
GES	Sacramento River Below Georgiana Slough	121.5234	38.2389
TSL	Threemile Slough at San Joaquin River	121.687	38.09
LIS	Yolo Bypass at Lisbon	121.587	38.475
DGL	Doughty Cut Above Grant Line Canal	121.425	37.815
DSJ	Dutch Slough at Jersey Island	121.671	38.013
GLC	Grantline Canal	121.5485	37.8196
HOL	Holland Cut near Bethel Island	121.5819	38.0164
LPS	Little Potato Slough at Terminous	121.4961	38.0964
MRU	Middle River at Undine Road	121.386	37.8339
NAUP	Middle River at Union Point	121.488361	37.890778
HLT	Middle River near Holt	121.5108	38.0031
ORQ	Old River at Quimby Is. near Bethel Is.	121.5645	38.0272
OAD	Old River Near DMC above dam	121.542	37.811
PRI	San Joaquin River at Prisoners Pt. near Terminous	121.5572	38.0594
SJG	San Joaquin River at Garwood Bridge	121.329	37.935
MSD	San Joaquin River at Mossdale Bridge	121.306	37.786

pattern in which turbidity generally decreases toward the deep, central part of the Delta, and increases upriver to the shallower north and south parts of the Delta. We then clustered sensor data by color according to the regions in Figure 2, and plotted turbidity as monthly and daily means over time (Figure 3). The distinct bands support the assumption that turbidity remains consistently proportional across regions. While turbidity varies across seasons, tides and years, we assumed that relative average turbidity between the stations does not change substantially in the Delta. We thus assigned a simple mean to each sensor, which was applied to the nearest *E. densa* sampling site for the model.

Statistical Modeling

We used mean water column depth, water velocity, and turbidity to estimate the probability of occurrence of *E. densa* at any given site. Though *E. densa* can grow densely enough to alter flows and turbidity within a stand (Santos et al. 2009; Yarrow et al. 2009), we assumed that our larger-scale estimates would provide sufficient relative accuracy to support the model.

We fit a series of generalized linear models using maximum likelihood, assuming a binomial distribution. The binomial distribution is appropriate for presence-absence data predicted by ordinal values (McElreath 2016). We used a logistic link to convert negative log-likelihood to probability (Bolker 2008;

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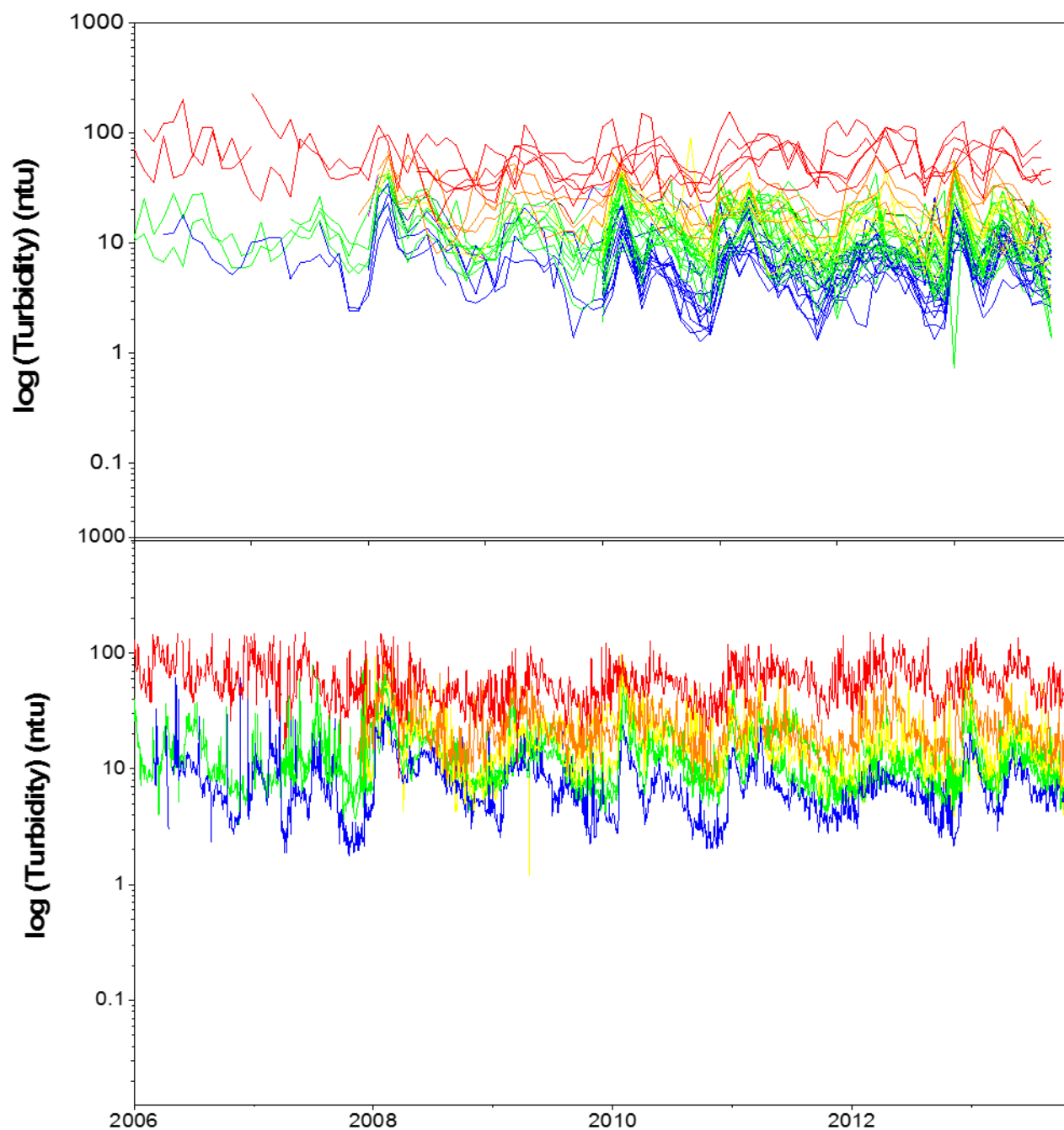


Figure 3 Above: Log mean monthly turbidity by station from 2006–2008. Below: Log mean daily turbidity for each turbidity zone from 2006–2008. Colors indicate geographic regions from which the data were obtained, corresponding with those in Figure 2.

Bolker et al. 2009; McElreath 2016). We eliminated sites that had incomplete or missing data, leaving 861 sites for the analysis (Figure 1). To fit the models, we used package *bbmle* (Bolker and R Development Core Team 2015) in Program R (R Development Core Team 2015). We compared model results using corrected Akaike Information Criteria (AICc) (Hurvich and Tsai 1989), which suggest the simplest models with the highest explanatory power (Akaike 1976). We then used R package *rethinking* (McElreath 2015) to sample proportionally over the highest performing models (m4 and m7) for a model-averaged posterior. We used the full posterior to estimate the mean predicted probabilities and high-probability density interval (HPDI), comparable to 95% confidence limits) for each parameter across the range of variable values (McElreath 2016). We used this approach rather than single-model null hypothesis testing in order to optimize the data over a range of models. We plotted the results as probabilities against the independent variables and evaluated them with respect to the data. In order to plot individual parameters for a multivariate model, all other variables must be held at a fixed value to evaluate individual effect. We used the means for water column depth (2.071 m), mean turbidity (10.722 NTU), and mean velocity (0.154 m s⁻¹).

RESULTS

We fit seven different models to the data using three different variables. The highest performing models (m4 and m7, see Table 2) had the lowest AICc values and together held over 99% of the models' weights. To evaluate our confidence in the fit, we drew 100,000 parameter values from the multivariate normal posterior density of both the selected models, using maximum a posteriori and variance-covariance. We used these draws to describe the model-averaged high density probability interval for the predicted mass of the posterior, in which 95% of the model predictions should occur. The selected model used depth², turbidity, and mean water velocity to predict *E. densa* occurrence.

$$y_i \sim \text{Binomial}(p_i, 1) \quad (1)$$

$$\text{Log} \frac{p_i}{1 - p_i} = \alpha + \beta_d D^2 + \beta_t T + \beta_v V$$

where:

y_i = predicted probability of *E. densa* occurrence

p_i = observed *E. densa* presence

α = intercept

β = slope coefficients

D = water column depth

T = mean turbidity

V = estimated mean water velocity

Maximum velocity proved to be a worse predictor than mean velocity and was eliminated from the model. More complex models that used the ratio or product of maximum to mean velocity predicted poor fits to the data, and were also eliminated.

The highest performing model results are shown in Table 3. Depth and turbidity have negative slopes with 95% confidence intervals well outside of zero, giving high confidence in these predictors. Mean velocity has a negative slope, with 95% confidence intervals covering the zero, offering low confidence in velocity as a predictor of *E. densa* occurrence.

Egeria densa was found as high as 1.1 m above MLLW, which was the upper extent of sampling. It was found as deep as a water column depth of 11 m MLLW. Because the depth data were fit with a square term, the plot of probability by depth has a changing slope. The 95% HPDI show a reliably negative slope (that is, a zero slope is precluded) from 2 to 10 m below MLLW (Figure 4). With all other variables fixed at their means, the peak probability of *E. densa*

Table 2 Top-performing models. AICc values, differences (dAICc), degrees of freedom (df) and model weights. The top performing models m4, m7, and m5 capture 100% of the weighting.

	AICc	dAICc	df	weight
m4	873.7	0.0	4	0.52
m7	873.9	0.2	5	0.48
m5	902.8	29.1	4	0.001
m6	917.6	43.9	4	<0.001
m3	921.2	47.5	3	<0.001
m2	940.3	66.6	3	<0.001
m0	949.2	75.5	2	<0.001
m1	951.2	77.5	3	<0.001

Table 3 Table of log-likelihood parameters for the highest performing models

	m4	5.5%	94.5%	m7	5.5%	94.5%
α	0.28	-0.09	0.64	0.42	0.01	0.82
β_d	-0.03	-0.04	-0.02	-0.03	-0.04	-0.02
β_t	-0.11	-0.15	-0.08	-0.11	-0.14	-0.07
β_v				-1.33	-2.91	0.24

α = intercept, β_d = depth, β_t = turbidity, β_v = mean

occurrence is 0.30 at a water column depth of 0 to 1 m below MLLW.

Egeria densa was found most frequently at sites that had low turbidities, typically below about 20 NTU (Figure 5). The negative slope and narrow HPDI sug-

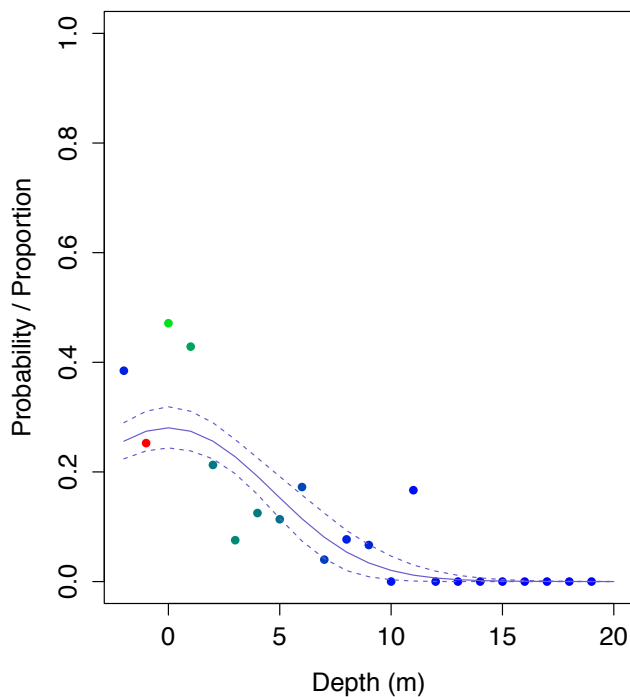


Figure 4 Effect of depth on probability of *E. densa* occurrence. The solid blue line is the probability of *E. densa* occurring at depth. The dotted blue lines are the high-density probability intervals (HDPI), which are equivalent to 95% confidence intervals for the predictions. Colored circles indicate the proportion of sites with *E. densa* present per binned depth level, using the color spectrum to indicate the relative number of observations at each level, where red represents the most observations, and blue the least observations.

gest that turbidity is a very good predictor of occurrence. The plant was found most commonly between 5 and 10 NTU, with steeply decreasing probability of occurrence at higher turbidity.

After accounting for the effects of depth and turbidity, mean velocity has only a weakly negative effect on probability of *E. densa* occurrence, with a 95% HPDI that includes a 0 slope (Figure 6). The plant occurs most commonly from about 0 and 0.5 m s⁻¹, but the model suggests that the apparent decrease in occurrence shown by the raw proportional data (colored circles) at higher velocities is better explained by the two other covariates: depth and turbidity.

DISCUSSION

We set out to test the hypothesis that the occurrence of the submersed aquatic plant *Egeria densa* in the

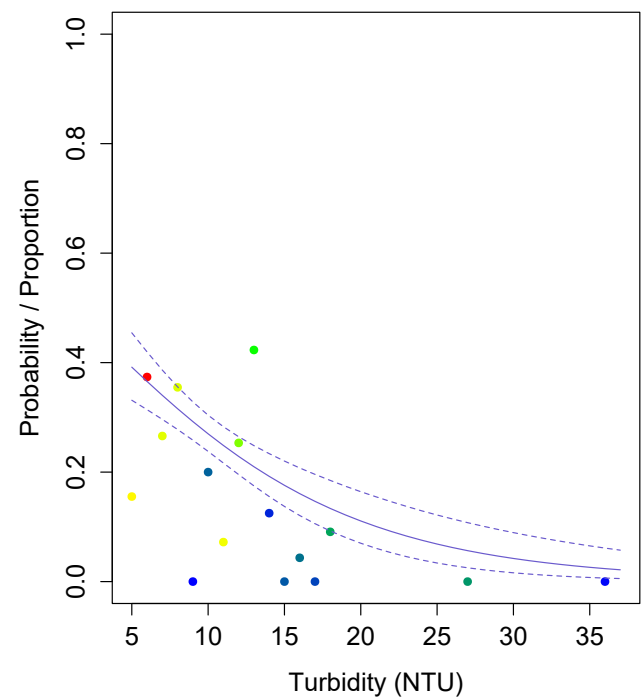


Figure 5 Effect of turbidity on probability of *E. densa* occurrence. The solid blue line is the probability of *E. densa* occurring at the estimated mean turbidity for each site. The dotted blue lines are the HDPI, which are equivalent to 95% confidence intervals for the predictions. Colored circles indicate the proportion of sites with *E. densa* present at the binned turbidity levels, using the color spectrum to indicate the relative number of observations at each level, where red represents the most observations, and blue the least observations.

Delta could be predicted using three key physical variables: depth, turbidity and velocity. Of the three, depth and turbidity had a clear effect. Increasing water column depth and turbidity both reduce the probability of occurrence. However, the model did not support an effect from water flow on *E. densa* at velocities found in the Delta in 2008, although research from outside the Delta has demonstrated a relationship.

The effect of depth varies in the Delta because *E. densa* requires immersion (Barko and Smart 1981; Hestir et al. 2008), limiting occurrence in shallow, intertidal waters; light attenuation from increasing depth and turbidity limits the lower range of occupancy (Bini et al. 1999; Bini and Thomaz 2005; Bornette and Puijalon 2011). In the Delta, the plant is found most commonly in lower intertidal to shallow

water habitat (between 1 m above MLLW and a water column depth of 2 m below MLLW) with the probability of occurrence decreasing with depth.

Turbidity had a strong effect across the range of values seen in the Delta, probably from light attenuation (Bini and Thomaz 2005; Hestir 2010). The probability of *E. densa* occurrence rapidly decreased from regions with a mean turbidity of 5 NTU to those with a mean turbidity of 15 NTU. *Egeria densa* was rarely found in regions with turbidities higher than 15 (only in 4 out of 122 sampled sites). The Delta has few sources of fine renewable sediment that increase turbidity, in large part because of water project operations, and this is one of a number of factors leading to increasing water clarity in the system (Wright and Schoellhamer 2004; Schoellhamer et al. 2013; Ferrari et al. 2014). This is particularly true in the central and south Delta (Figure 2), where *E. densa* is notably abundant. The establishment of *E. densa* and other aquatic macrophytes creates local changes in water quality, because large, dense stands slow water velocity, shade out phytoplankton, increase temperatures and filter sediment from the water column (Madsen et al. 2001; Santos et al. 2009; Yarrow et al. 2009). Such conditions provide a feedback loop that favors *E. densa*, promoting expansion of its range. This is consistent with the increasing rate of *E. densa* expansion in the Delta. In the 70 years since its introduction, it has become obviously invasive only in the past 20 years.

The model shows no effect of mean or maximum water velocity on probability of *E. densa* occurrence. This is somewhat surprising, because many aquatic macrophytes are positively associated with flow velocities of 0.3 to 0.4 m s⁻¹, and constrained by flow velocities of > 1 m s⁻¹ (Chambers et al. 1991; Lacoul and Freedman 2006). *Egeria densa* occurrence has been found to be sensitive to water velocities approaching 0.39 m s⁻¹ (Gantes and Caro 2001). Both mean and maximum velocities in the Delta can bracket these speeds (modeled mean flows for 2007 ranged from 0.001 m s⁻¹ to 0.524 m s⁻¹; modeled maximum velocity ranged from 0.007 m s⁻¹ to 1.026 m s⁻¹). However, water movement can have complex interactions with aquatic macrophytes. Though increasing velocity can negatively affect biomass and growth, flows can also provide opportunities for gas exchange and nutrients (Bornette

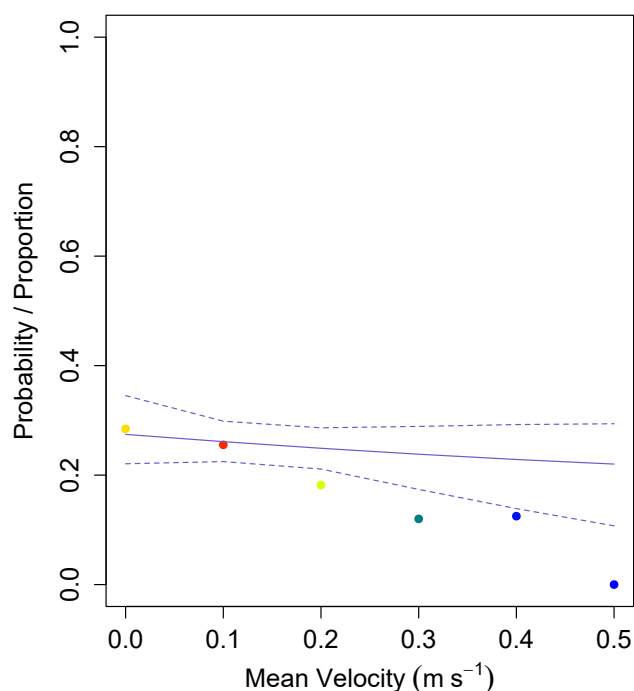


Figure 6 Effect of mean velocity on probability of *E. densa* occurrence. The solid blue line is the probability of *E. densa* occurring at the estimated mean velocity for each site. The dotted blue lines are the HDPI, which are equivalent to 95% confidence intervals for the predictions. Colored circles indicate the proportion of sites with *E. densa* present at the binned mean velocity levels, using the color spectrum to indicate the relative number of observations at each level, where red represents the most observations, and blue the least observations.

and Puijalon 2011), and even assist in the spread of propagules (Madsen et al. 2001). In addition, the tidal nature of the Delta differs greatly from stream flows, because peak sustained directional velocities rarely occur for more than the 4 or 5 hours between slack tides. Although there were insufficient data to provide support for the hypothesis that high flows reduce the probability of *E. densa* occurrence, it is worth noting that *E. densa* never occurred in sites with a mean velocity of greater than 0.427 m s^{-1} ($n=5$), or a maximum velocity greater than 0.792 m s^{-1} ($n=33$). This would be consistent with an upper threshold, one that might be slightly higher in the tidal Delta than in riverine systems (Hestir 2010). Water year 2008 was a critically dry year for central California, resulting in lower than usual outflows (Figure 7); higher winter and spring outflows might provide a wider range of values for flow, which

would result in a different outcome than in the present study.

CONCLUSION AND MANAGEMENT IMPLICATIONS

Egeria densa is widely distributed in sloughs and channels throughout the Delta, often longitudinally along the edge at optimal depth, and decreasing in density toward the deeper channel center. A typical pattern of *E. densa* distribution in the Delta can be seen in Figure 8. This photo was taken during late spring of 2013 at a very high tide in a slough with approximately concave bathymetry. The band of vegetation at the surface shows the approximate location of rooting along the shallow edge of the channel. On the landward (left) side of the band, the plants are probably limited by exposure, leaving a patch of open water between the bank and the stand of *E.*

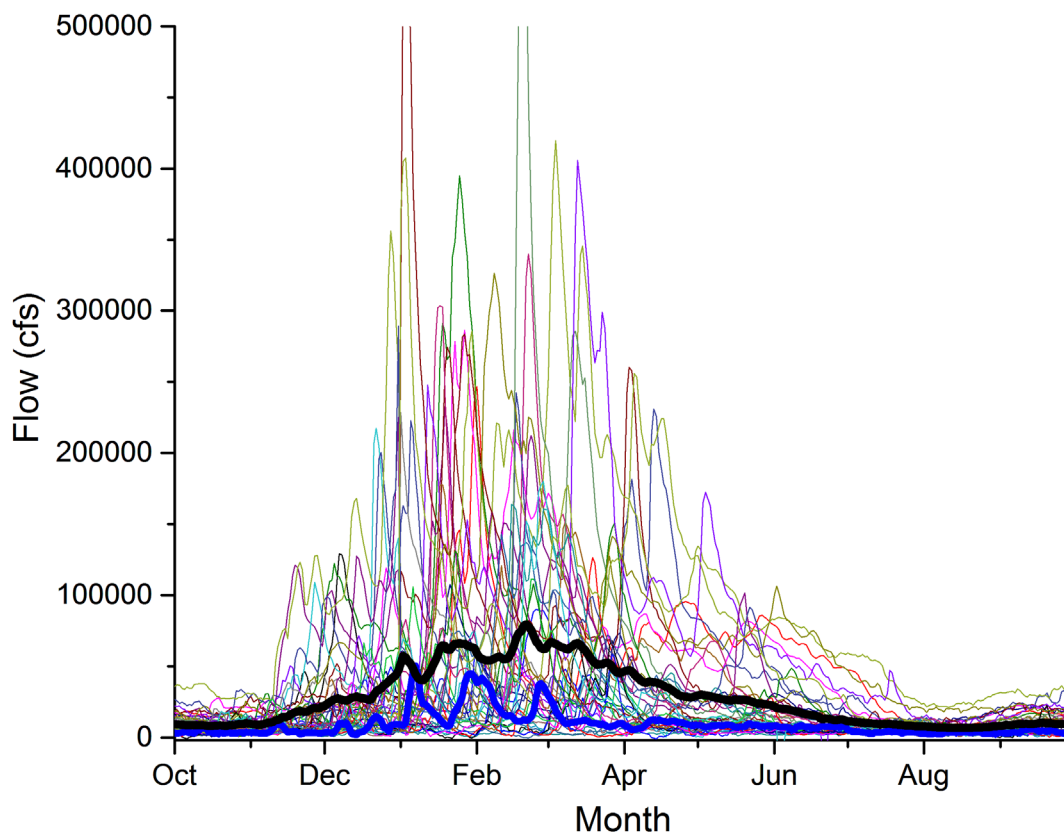


Figure 7 Delta mean net daily outflow from water years 1966 to 2008 (black line). Colored lines represent different years; 2008 is the dark blue line. Water year 2008 was a critically dry year, and outflows were low across all months relative to the mean.



Figure 8 *Egeria densa* growing along the shallow margins of Lindsey Slough in June 2008. It is limited on the shore-side by drying; on the channel-side by depth and water movement (Photo: Amy Chandos).

densa. On the mid-channel (right) side of the band, the plants are limited by depth and turbidity; that is, by light penetration. By late August, the stalks form a canopy that covers a much wider area, giving the visual impression that it is established much more broadly. This is illustrated in the conceptual model of *E. densa* habitat usage shown in Figure 9. Drying and light limitation by depth are the two main controls over vertical plant distribution, promoting a band with a high probability of occurrence, surrounded by open water on the shore-side and channel-side. In regions with higher turbidity, the band contracts, because of increased light limitation. Steep slopes may create narrower bands than broad, shallow slopes because of the difference in optimal substrate area.

Ironically, restoration projects in the Delta put high value on shallow water and intertidal restoration habitats (ICF International 2013), which overlap greatly with the optimal depth distribution of *E. densa* (BDCP 2013). Shallow water habitat offers useful ecosystem benefits when restoration is successful, including:

1. potentially high phytoplankton productivity resulting from increased exposure to the photic zone;
2. low bivalve presence, potentially allowing pelagic productivity to be accumulated and “exported” to other regions of the Delta (Lopez et al. 2006; Durand 2015);
3. the ability to harness tides to drive exchange of nutrients and organisms between wetlands and

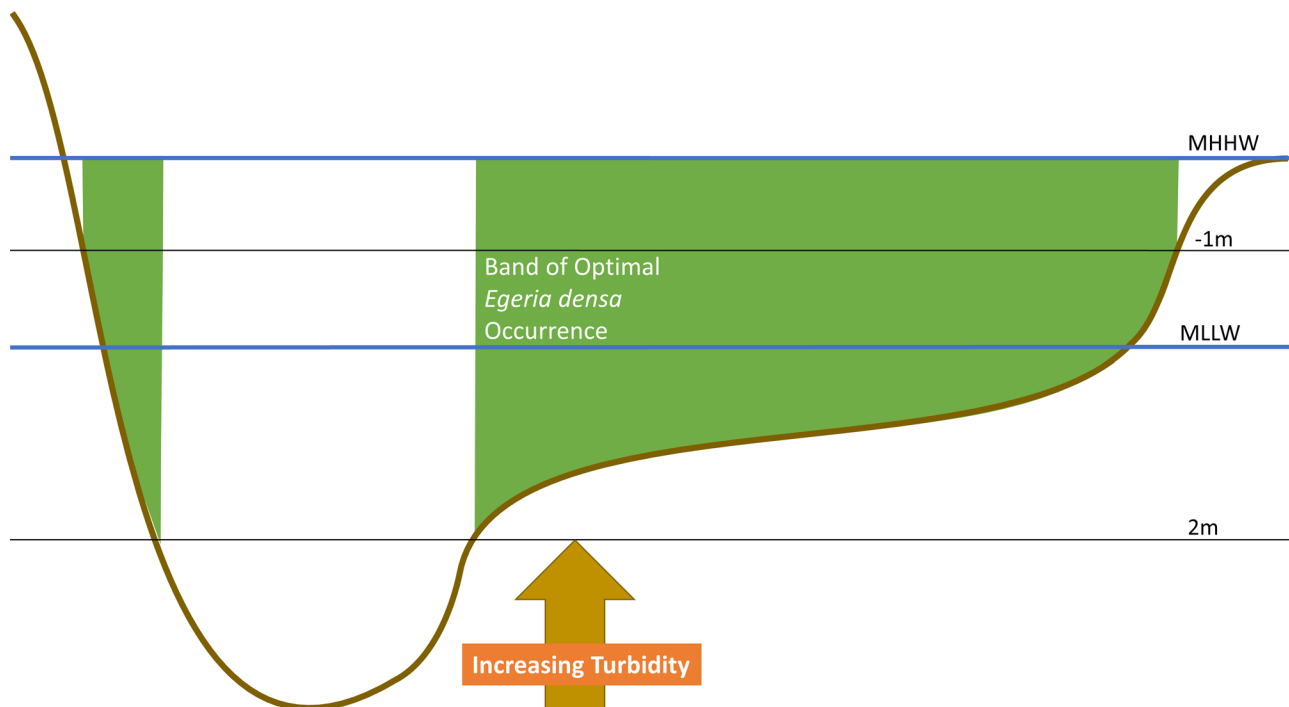


Figure 9 Conceptual model of *Egeria densa* distribution across channel depth. The highest probability of occurrence is in the green shaded areas above the brown curve, which represents bathymetry in relationship to sea level. Mean lower low water (MLLW) and mean higher high water (MHHW) are shown as a blue horizontal bars. The black bars represent the depth range of the plant, from 1 m above MLLW to a depth of 2 m below MLLW. As turbidity increases, it shades out *E. densa*, decreasing its lower depth range (in effect, pushing “up” the lower depth bar), resulting in less horizontal coverage.

channels (Ahearn et al. 2006; Enright et al. 2013); and

4. foraging and refuge opportunities for fish and waterfowl.

However, such desirable traits must be weighed against the probability of *E. densa* establishment, which may interfere with these benefits. Benefits to pelagic productivity and habitat may be difficult to realize if new restoration projects maximize depths in the range of –1 to 2 m below MLLW.

Limited options exist for managing *E. densa* in restorations. Herbicide application is used extensively in the Delta, and it may be effective for short periods of time in hydrodynamically isolated areas (Santos et al. 2009). However, herbicides may have unintended effects on other organisms—particularly phytoplankton and invertebrates—that are supposed to be supported by restoration (Yarrow et al. 2009).

Increasing turbidity may have the most powerful effect on limiting *E. densa*, but sources of sediment are increasingly scarce in the Delta. The north Delta receives sediment inputs from the Yolo Bypass during wet years, and these may be important to controlling the plant in the region around Cache and Lindsey sloughs and Liberty Island. However, the current drought has brought an expansion of the plant in the region (personal observation), and it is currently unknown what effects a wet year and Yolo Bypass sediment will have on this range expansion. Securing sediment contributions from outside sources, if they are no longer delivered by nearby rivers in the Delta, may be an important factor in maintaining the integrity of restoration sites.

Gating of select restoration sites may offer some control over undesirable developments, and would provide opportunities for experimentation as well. Gating allows manipulation of flows and residence time, nutrient concentrations, and turbidity. It also

offers the opportunity to drain and dry out restoration sites when they have become infested with undesirable organisms. Such an approach may be useful for controlling the abundance of the invasive clams *Potamocorbula amurensis* and *Corbicula fluminea* and undesirable centrarchid fishes, as well as unwanted aquatic vegetation such as *E. densa* (Bini and Thomaz 2005) or water hyacinth (*Eichhornia crassipes*), while allowing re-introduction of native organisms to “reset” an unsuccessful successional progression at the restored site.

Although the effect of flows is inconclusive from this data set, research from rivers and local anecdotal observations suggest a negative effect at higher flows than were studied here. Given that flow management is an important piece of ongoing Delta restoration, this question should be resolved soon, using plant distribution data across years of varying flows. The range of *E. densa* expanded after the droughts of the 1980s and 1990s, and understanding the mechanism behind this expansion is important for predicting the effects of the current drought, as well as long term changes from climate change. Factors other than flow may have had a greater effect, including increased water clarity. Other important factors that should be considered are the effects of previous occupancy (Santos et al. 2011), increased temperatures, and changing nutrient concentrations (Glibert et al. 2011).

Sea level rise will cause the Delta to become deeper, saltier and warmer, and turbidity will continue to decline (Wright and Schoellhamer 2004). Extreme weather events will become more common, including extremes of high and low flows (Cloern et al. 2011). Active sculpting of channels to support restoration is necessary, but depths will increase by 1 to 1.5 m within the next 100 years. These changing conditions will cause *E. densa* to expand its range away from the deepest and most brackish parts of the Delta, and into the fresh, shallow water periphery of the Delta. As new shallow water habitats are formed, there is a high likelihood that they will be colonized by *E. densa*, which will dominate the ecological character of these transitional regions.

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