Estuaries and Coasts
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Salinity Tolerance and Competition Drive Distributions of Native and Invasive Submerged Aquatic Vegetation in the Upper San Francisco Estuary

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Abstract Both abiotic and biotic factors govern distributions of estuarine vegetation, and experiments can reveal effects of these drivers under current and future conditions. In upper San Francisco Estuary (SFE), increased salinity could result from sea level rise, levee failure, or water management. We used mesocosms to test salinity effects on, as well as competition between, the native *Stuckenia pectinata* (sago pondweed) and invasive *Egeria densa* (Brazilian waterweed), species with overlapping distributions at the freshwater transition in SFE. Grown alone at a salinity of 5, *E. densa* decreased fivefold in biomass relative to the freshwater treatment and decomposed within 3 weeks at higher salinities. In contrast, *S. pectinata* biomass accumulated greatly (~4× initial) at salinities of 0 and 5, doubled at 10, and was unchanged at 15. When grown together in freshwater, *S. pectinata* produced 75 % less biomass than in monoculture and significantly more nodal roots (suggesting increased nutrient foraging). At a salinity of 5, a decline in *E. densa* performance coincided with a doubling of *S. pectinata* shoot density. Additional experiments on *E. densa* showed elevated temperature (26 and 30 °C) suppressed growth especially at higher salinities (≥5). We conclude that salinity strongly influences distributions of both species and that competition from *E. densa* may impose limits on *S. pectinata* abundance in the fresher reaches of SFE. With a salinity increase of 5, *S. pectinata* is likely to maintain its current distribution while spreading up-estuary at the expense of *E. densa*, especially if increased temperature also reduces *E. densa* biomass.

Keywords Climate change · SAV · San Francisco Estuary · Salinity · Temperature · Aquatic plant

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Introduction

Species distributions along strong abiotic gradients are determined largely by differential tolerances to environmental stressors but can also be influenced by biotic interactions (Purer 1942; Connell 1972; Paine 1974; Dunson and Travis 1991). In estuaries, the gradient in salinity from ocean to river leads plant species to sort in order of their capacities to withstand or avoid osmotic stress (Odum 1988), along with their abilities to compete for space or other resources in increasingly fresher, and presumably more benign, conditions (Crain et al. 2004). Effective conservation and management of estuarine plant assemblages rely upon understanding the forces that regulate them, especially as human actions lead the abiotic and biotic context of the habitat to change in multiple ways.

Changes in estuarine conditions are underway at both global and local scales. Global climate change is leading rising seas to push saline waters up estuaries while the greenhouse effect increases temperatures (Titus et al. 1991; Scavia et al. 2002; Walther et al. 2002; Najjar et al. 2010). Use and management of freshwater is shifting the timing and magnitude of salinity fluctuations in estuarine waters (Cloern and Jassby 2012; Jiang et al. 2014). Biotic interactions are also changing through the introduction of nonnative species (Vitousek et al. 1997; Cohen and Carlton 1998), some of which exhibit wider

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abiotic tolerances than native species (Hershner and Havens 2008). Experimental manipulations are needed to understand the relative importance and interactive effects of abiotic and biotic factors in determining estuarine plant distributions and dynamics.

We sought to understand factors that determine the abundance and distribution of native submerged aquatic vegetation (SAV) currently, as well as under future scenarios of climate change and water management in the heavily invaded San Francisco Estuary (hereafter, SFE). In the open waters of SFE, the low-salinity region known as Suisun Bay (Fig. 1) contains over 485 ha (1200 acres) of native pondweeds in the genus *Stuckenia* (Boyer et al. 2012). Dominated by *Stuckenia pectinata* (sago pondweed), these beds are sparse in the lower water column but form a canopy near the surface. In SFE, *S. pectinata* beds occur along the migratory path for a number of native fish species (Nichols et al. 1986), which may forage on the abundant invertebrates on these plants (Boyer, unpublished data).

The distribution of *S. pectinata* extends east (up-estuary) into the western reaches of the Sacramento-San Joaquin Delta (hereafter, Delta), where the dominant SAV species is *Egeria densa* (Brazilian waterweed) (Santos et al. 2011). Likely introduced through hobbyists' aquaria (Marin et al. 2009), *E. densa* in the Delta grows in large, dense mats that choke channels (Johnson 2006) and can form monospecific stands (Santos et al. 2011), leading the CA Invasive Plant Council and the CA Department of Food and Agriculture to categorize it as a threat species. Unlike *S. pectinata*, *E. densa* forms dense beds that can reduce local turbidity and create shadowy hiding places for predators of small fish including native fish species of concern (Anderson 1990; McGowan and Marchi 1998; Nobriga et al. 2005; Lund et al. 2007).

The shift from *S. pectinata* to *E. densa* dominance from Suisun Bay into the west Delta suggests that salinity changes along this axis influence the abundance and distribution of the two species. A few studies from other regions support this observation; *S. pectinata* is known to tolerate salinities as high as 12 (Teeter 1965; Hall et al. 1997), whereas salinity levels as low as 5 have been shown to negatively affect *E. densa* in its native Chile (Hauenstein and Ramirez 1986).

If salinity is a strong determinant of these species' distributions currently, then predicted salinity increases in SFE would be expected to alter their positions up-estuary along the salinity gradient. Salinity could increase in Suisun Bay and the Delta through several mechanisms stemming from climate change and water management. Sea level rise and shifts in magnitude and timing of snowmelt events are projected to

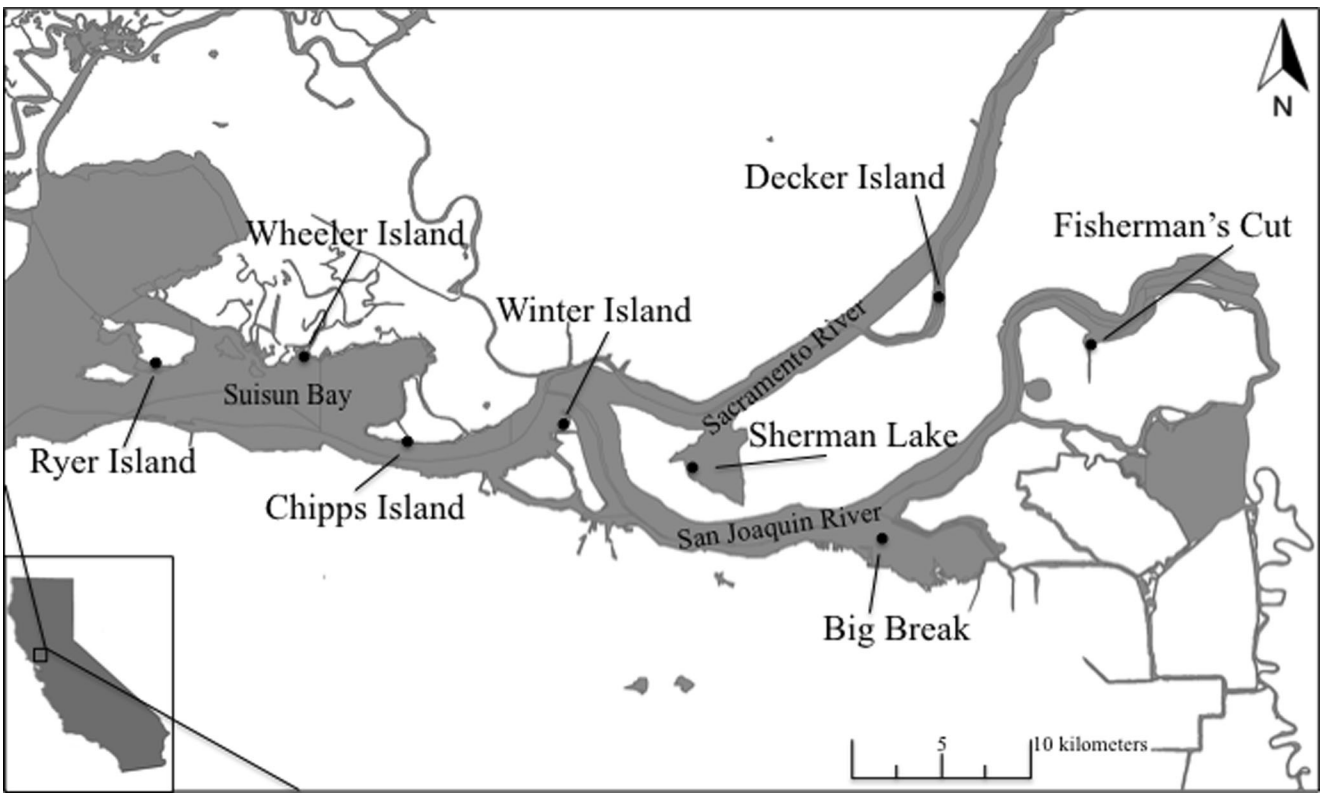

Fig. 1 Map of field sites in the upper San Francisco Estuary, CA, USA, where water quality measurements were taken over 1 year. *Ryer*, *Wheeler*, *Chipps*, and *Winter Islands* are *S. pectinata*-dominated sites. Winter Island is near the confluence of the Sacramento and San Joaquin Rivers, with the Delta region spreading east from this point. *Sherman Lake*, *Big Break*, *Fisherman's Cut*, and *Decker Island* are *E. densa*-dominated sites

increase salinity levels by 1–3 in the vicinity of Suisun Bay by 2090 (Knowles and Cayan 2002). In addition, extended periods of drought could lead to increased salt penetration not counteracted by reservoir releases during the summer months. There is also potential for levee failures through erosion or earthquakes, leading to a higher volume of saline tidal waters reaching up-estuary. Finally, management actions that inadvertently or deliberately reduce fresh water releases during the dry season could increase salinity in this region. Summer and fall salinity has already increased in the last 25 years due to management of fresh water releases from water control structures (Knowles and Cayan 2002; Contra Costa Water District 2009). C&H Sugar Refining Company (Crockett, CA) has long tracked salinity in order to access fresh water for its refining process; its data show annual salinity intrusion now occurs much earlier in the year in Suisun Bay (beginning of March) compared to the early 1900s (beginning of July) (Water Resources Department 2010).

Temperature is also projected to rise in the Estuary due to climate change. Mean annual air temperatures are expected to increase by 2 °C by 2090, and daily minimum and maximum water temperatures are also projected to increase in Suisun Bay and the western Delta (Knowles and Cayan 2002; Wagner et al. 2011). Changes in temperature may not have a drastic effect on *S. pectinata* and *E. densa* abundance and distributions in the near future, as previous studies from other regions indicate both can withstand temperatures of 30 °C or higher (Barko and Smart 1981; Spencer and Anderson 1986; Pilon and Santamaria 2002; Wersal et al. 2006). However, little is known of temperature ranges or tolerances within SAV beds of the upper San Francisco Estuary.

We used mesocosm experiments to elucidate the roles of salinity and competition in determining distribution and abundance of the dominant SAV species in Suisun Bay (*S. pectinata*) and the Delta (*E. densa*) and to predict how patterns may shift in a future of higher salinity within the region. The mesocosm experiments tested (1) salinity tolerance of *S. pectinata* and *E. densa* alone and in combination and (2) salinity tolerance of *E. densa* under a range of temperatures. In addition, we used salinity and temperature monitoring to describe the seasonal ranges currently found within Suisun Bay and west Delta SAV beds and to parameterize levels of these factors to use in mesocosm experiments. We hypothesized that *E. densa* is limited to the fresh waters of the Delta by its low tolerance to salinity, while *S. pectinata* is primarily found in the brackish waters of Suisun Bay because it does not compete well with *E. densa* in freshwater. In addition, we expected *E. densa* to withstand high temperatures in freshwater but to become increasingly stressed with increased salinity and temperature together.

Methods

Study Region and Experimental Approach

The San Francisco Estuary is a hydrologically dynamic system, receiving tidally driven marine inputs and riverine-driven freshwater inputs with seasonal freshwater peaks during winter and spring storms (Kimmerer 2002). Humans have drastically altered the natural flow patterns of the system by developing dams, diversions, and canals upstream (Nichols et al. 1986). Salinity variability is largely driven by storm inputs in the winter and the amount of freshwater released from reservoirs for export to farms and cities of central and southern California in the summer (Enright and Culberson 2009).

Within Suisun Bay, SAV is dominated by sago pondweed (*S. pectinata*) according to molecular genetic analyses (Patten and Boyer, unpublished data); although the plants are larger and less branched than is typical of the species, the pondweed family is known to be highly plastic (Kaplan 2002). *S. pectinata* has a pseudo-annual life cycle, i.e., it is a perennial clonal plant that also behaves as a vegetatively reproducing plant annual (Van Wijk 1988). *S. pectinata* produces overwintering tubers as well as turions (buds) that are buried in the sediment in winter and remain dormant until favorable conditions return (Rybicki et al. 2001; Triest et al. 2010).

Heading east into the Delta, the SAV assemblage includes native submerged aquatic plants, including *S. pectinata*, *Ceratophyllum demersum* (coontail), *Elodea canadensis* (common waterweed), and *Potamogeton nodosus* (American pondweed), but also harbors numerous introduced species, with *E. densa* the most invasive (Santos et al. 2011). *E. densa* is a successful invader around the world, in part due to high phenotypic plasticity and its ability to reproduce asexually using fragments (Haramoto and Ikusima 1988; McCollough 1997; Riis et al. 2010; Santos et al. 2011).

Field Salinity and Temperature

We assessed the salinity and temperature ranges in four locations dominated by each species. *S. pectinata*-dominated sites in Suisun Bay and the west Delta included Ryer, Wheeler, Chipps, and Winter Islands (Fig. 1). *E. densa*-dominated sites in the western and central Delta included Big Break, Sherman Lake, Fisherman's Cut, and Decker Island. Measurements were taken every 15 min for over 1 year (starting October 2011) using Hobo Conductivity Data Loggers (Model U24-001) deployed at ~30-cm depth. Occasional data gaps occurred due to fouling, damage from boats, or loss of instruments. Seasonal averages were calculated for all remaining data until December 2012.

Salinity Tolerance and Competition

A mesocosm experiment was conducted to determine the influence of salinity on growth of and competition between *S. pectinata* and *E. densa*. There were four salinity treatments (0, 5, 10, 15) and three vegetation treatments (each species alone or together), in a fully crossed design. Salinities were chosen to represent the range in average salinity for summer/fall in Suisun Bay (~2–9) and the Delta (~0–1), and ~5 units above the highest average measured (~1 unit above maximum Suisun Bay salinity; see "Results"). This was a replacement design (Harper 1977) in which all mesocosms started with ~50 g (wet weight) of plant tissue, with the mixed treatment containing ~25 g of each species (average biomass for all tanks was 48 g ± 0.8 [SD]). Apical shoots were used for *E. densa* (no roots), and whole shoots were used for *S. pectinata* with 2–8 cm of root material (negligible weight). The experiment lasted 3 months (June through August 2012), long enough to detect interactions between species and short enough to minimize artifacts of high biomass (Gibson et al. 1999).

The experiment was conducted in a greenhouse at the Romberg Tiburon Center, San Francisco State University's estuarine research and teaching facility in Tiburon, CA. Each treatment had 5 replicates for a total of 60 mesocosms in a complete randomized design. *S. pectinata* shoots were collected at Ryer Island and *E. densa* shoots were collected at Decker Island, locations where each species forms monospecific stands. Plants were rinsed of all visible epibiota and grown in 200-L translucent polyethylene tanks (55.9 cm D × 87.6 cm L) in tap water at a depth of 60 cm. Premier For Plants (Seachem in Madison, GA) was added to each mesocosm prior to planting to remove chlorine/chloramine. Once per week, salinity was measured and freshwater added to counter evaporation. A sandy-loam terrestrial soil (American Stone and Soil, San Rafael, CA) 7 cm deep was inoculated with field sediment (equivalent to ~0.3 % of the total substrate) to include the natural microbial assemblage. Mesocosm temperatures, measured 1×/week, ranged from 19 to 27 °C with an average of 21 °C (0.5 SD). Mesocosms under the greenhouse roof received solar irradiance of 438 ± 33 (SD) μmol quanta m^2 s^{-1}, measured just below the water's surface weekly at midday, with a range of 221–599 across 60 individual measurements. These irradiance levels were considered sufficient for growth, as they are well above those measured in Suisun Bay *S. pectinata* beds (range 76–333 μmol quanta m^2 s^{-1}) near the surface at the lowest tides (Boyer, unpublished data). The uncoated polycarbonate roof is expected to have permitted UV transmission similar to field conditions.

We placed Flourish Tabs (Seachem; 0.28 % nitrogen [N] and 0.17 % phosphorus [P]) into the sediment to deliver ~0.02 μM N and 0.006 μM P over the 3 months. This was intended to provide nutrient-sufficient conditions much lower than in the field (Wilkerson et al. 2006). Still, epiphytic algal biomass grew within the first month, and we added 2–5 *Physa* sp. snails (from a culture tank of Delta plants) to each mesocosm, which reduced algae from the tank walls and leaf surfaces.

Percent change in biomass, shoot number, number of inflorescences, and nodal root biomass were quantified at the end of the experiment. Belowground biomass and nodal roots were separated from aboveground tissues prior to any analysis. All vegetative tissues were weighed wet, then dried at 50 °C for ~48 h and weighed. To calculate percent change in dry aboveground biomass over the 3-month experiment, initial dry weight was estimated using a regression of final wet and dry weights (*S. pectinata*: $y = 0.0595x + 3.84$, $n = 29$, $R^2 = 0.84$; *E. densa*: $y = 0.0934x + 1.59$, $n = 19$, $R^2 = 0.95$). We also examined change in wet *E. densa* mass, which showed larger differences than dry mass. For mixed culture treatments, below- and aboveground (nodal) root, turion, and inflorescence data were doubled due to starting with half the biomass.

We used Kendall's tau to detect responses to salinity of each species grown in monoculture; this provided a measure of strength (correlation) of the relationship between each response variable and salinity (Sen 1968). A Mann-Whitney *U* (MWU) test compared *S. pectinata* inflorescence production between salinities of 0 and 5.

To evaluate competition, we tested overall performance of *S. pectinata* with and without *E. densa* present using a multivariate analysis of variance (MANOVA) on growth responses (aboveground biomass, shoot number, and root biomass). To test whether competition was occurring at specific salinity levels, *t* tests were used to compare mono- and mixed *S. pectinata* cultures for shoot number, root biomass, nodal root biomass, and turion and inflorescence counts. Aboveground biomass did not meet parametric test assumptions and a MWU test was substituted.

Due to high mortality in response to salinity, competition patterns for *E. densa* were only assessed at the 0 salinity level. *t* tests were used to analyze differences between mono- and mixed cultures for shoot number, root biomass, and inflorescence counts. Shoot biomass data did not meet assumptions of parametric tests and a MWU test was used instead.

Temperature and Salinity Experiment on *E. densa*

As *E. densa* can spread by fragments, these were used in smaller mesocosms to test salinity effects in a temperature-controlled room (not possible with *S. pectinata*). *E. densa* was grown in 20-L aquaria at three temperatures that represent typical average summer temperatures (22 °C; see "Results") and potential future temperatures of the Delta (26 and 30 °C), which are also reached currently at times (see maximum temperatures in Results). Temperature treatments were run

separately with each experimental round lasting 6 weeks. There were four salinity treatments (0, 5, 10, and 15) with five replicates of each (20 mesocosms per temperature round) in a randomized, complete block design. Experimental rounds were conducted in December 2012 to January 2013 (22 °C), February to March 2013 (26 °C), and April to May 2013 (30 °C). Four apical (tip) sections of *E. densa* shoots were cut to 30 cm and planted in each mesocosm. Experimental conditions were consistent with the salinity/competition experiment except for container size and the artificial light provided by six 34-watt grow lights on a 12-h day/night cycle (~100 μM quanta m^{-2} s^{-1}). The same plant responses were measured at the beginning and end of each round as in the salinity/competition experiment. Fresh tissue (wet weight) was used to determine biomass responses. For each experimental round, a one-way ANOVA was used to test for the effect of block (position in the room); finding none ($p > 1.0$), block was excluded thereafter. To test the interaction of salinity and temperature, a two-way ANOVA was used for wet biomass. Scheirer-Ray-Hare (SRH) tests were used for shoot and root length as those measures did not meet assumptions of parametric tests.

Because each temperature treatment was run at a different time, temperature effects could have been confounded by other factors that differed with time; therefore, we ran a "control experiment" with all temperature treatments using Aqueon submersible aquarium heaters (200 W) at one salinity level (5). There were 15 mesocosms (3 temperatures × 1 salinity × 5 replicates) in this 6-week (July-August 2013) experiment. We visually compared patterns in this control experiment to the treatment with a salinity of 5 from the separate temperature runs in the experiment described above. In addition, two one-way ANOVAs were used to test temperature effects on *E. densa* grown in the control experiment and in the temperature experiment at a salinity of 5, each followed by a Tukey's HSD test.

Results

Field Salinity and Temperature

Field measurements reflected the expected west–east salinity gradient from brackish in Suisun Bay to fresh in the Delta (Table 1). Salinities in the *S. pectinata*-dominated sites in Suisun Bay ranged from nearly fresh to brackish (0.5–13.9; Table 1). Most *E. densa*-dominated sites remained near fresh throughout the seasons (maximum 3.6 in fall; Table 1). Seasonal temperature trends among all Suisun Bay and Delta sites were similar, ranging from 9.4 to 30.9 °C across sites (Table 1).

Salinity Tolerance and Competition Experiment

Salinity Responses in Monoculture

E. densa increased dramatically in biomass and shoot number over the course of the 6-week experiment in freshwater (500–1000 %, Fig. 2). However, at salinities above 0, *E. densa* declined greatly in biomass, shoot number, and root biomass (Fig. 2). At a salinity of 5, the biomass of *E. densa* was 10× lower than in the freshwater treatment; no tissues remained at salinities of 10 or 15.

When grown alone in freshwater, *S. pectinata* shoot and root biomass also increased greatly (>10×) over time, as did shoot number (4×) (Fig. 2). *S. pectinata* produced similar biomass and shoot counts at a salinity of 5 as at 0 but less at higher salinities (Fig. 2). Still, at a salinity of 10, *S. pectinata* biomass doubled and shoot number increased sixfold from initial levels. At a salinity of 15, biomass and shoot number remained comparable to initial levels, although these were new shoots that emerged following senescence of the original shoots within the first month of the experiment. *S. pectinata* produced 5× more inflorescences at a salinity of 5 than at 0 (average of 4.8 and 1 inflorescences, respectively; MWU test, $p = 0.05$; Fig. 3c), but none were produced at salinities of 10 or 15. There was no difference in turion production with increased salinity.

Performance in Mixed Culture

Overall, the presence of *E. densa* limited *S. pectinata* performance across response variables (MANOVA, $p = 0.001$). In freshwater, *S. pectinata* produced significantly less biomass in mixed culture than in monoculture (*t* test, $p = 0.007$; Fig. 4a) and tended to produce less root biomass (Fig. 4c). *S. pectinata* also produced significantly more aboveground, adventitious roots from its nodes (nodal roots) in the freshwater, mixed culture (*t* test, $p = 0.013$; Fig. 3a). Further, in all salinity treatments, *S. pectinata* tended to produce fewer turions in mixed culture than in monoculture, significantly so at salinities of 0 and 15 (*t* tests, $p = 0.018$ and 0.005, respectively; Fig. 3b). In contrast, at a salinity of 5, *S. pectinata* produced ~2× greater shoot densities (*t* test, $p = 0.03$) and tended to have greater root biomass in mixed culture than in monoculture (Fig. 4 b, c).

Large declines in *E. densa* biomass at salinities above 0 (Fig. 4c) limited our comparisons of mixed versus monoculture performance to the freshwater treatment. For this treatment, trends were opposite to those of *S. pectinata*; *E. densa* produced ~2× more wet biomass in mixed culture than in monoculture (*t* test, $p = 0.03$, data not shown) and also tended to produce greater dry biomass and shoot numbers (Fig. 4 a, b).

Table 1 Average and maximum salinity and temperature from the eight sites over time

	Date range	Average salinity	Max salinity	Average temp. (°C)	Max temp. (°C)
Ryer Island					
Fall 2011	ND	ND	ND	ND	ND
Winter	December 1–13, 2012	6.1	9.7	10.3	12.4
Spring	April 1– May 30, 2012	2.0	6.7	18.7	21.2
Summer	June 1 – August 30, 2012	6.6	10.2	20.9	26.7
Fall	September 1 – November 30, 2012	9.0	11.4	17.8	22.8
Wheeler Island					
Fall 2011	October 24 – November 30, 2011	3.3	8.1	14.2	27.6
Winter	December 1, 2011 – February 28, 2012	3.6	8.0	9.8	15.3
Spring	March 1 – May 30, 2012	1.0	5.9	15.7	23.4
Summer	June 1 – July 31, 2012	4.7	8.9	21	29.3
Fall	ND	ND	ND	ND	ND
Chipps Island					
Fall 2011	October 24 – November 30, 2011	3.0	8.2	14.6	20.3
Winter	December 1, 2011 – February 28, 2012	3.2	11.0	9.6	14.2
Spring	March 1 – May 30, 2012	0.6	5.7	15.7	22.4
Summer	June 1 – August 30, 2012	3.4	13.9	21.1	24.8
Fall	September 1 – November 30, 2012	5.7	10.7	18.1	22.3
Winter Island					
Fall 2011	October 24 – November 30, 2011	1.7	5.8	15.9	19.1
Winter	December 1, 2011 – February 28, 2012	2.0	6.5	9.8	17.3
Spring	March 1 – May 30, 2012	0.5	4.8	15.7	22.6
Summer	June 1 – August 30, 2012	2.2	6.5	21.3	27.5
Fall	September 1 – November 30, 2012	6.4	9.6	16.5	23.1
Sherman Lake					
Fall 2011	October 24 – November 30, 2011	0.2	1.2	15.1	30.2
Winter	December 1, 2011 – February 28, 2012	0.6	2.2	9.6	21.9
Spring	ND	ND	ND	ND	ND
Summer	June 1 – August 30, 2012	0.5	1.8	22.3	30.9
Fall	September 01 – November 30, 2012	1.3	3.6	18.6	23.4
Big Break					
Fall 2011	October 24 – November 30, 2011	0.2	0.6	15.1	21.8
Winter	December 1, 2011 – February 28, 2012	0.5	1.7	9.7	17.3
Spring	ND	ND	ND	ND	ND
Summer	June 1 – August 30, 2012	0.03	0.5	23.2	27.6
Fall	October 1 – November 30, 2012	0.5	1.7	17.6	21.2
Fisherman's Cut					
Fall 2011	ND	ND	ND	ND	ND
Winter	December 1, 2011 – February 28, 2012	0.3	0.6	9.4	17.1
Spring	March 1 – May 30, 2012	0.1	0.6	16.0	28.2
Summer	June 1 – August 30, 2012	0.1	0.7	22.4	30.7
Fall	ND	ND	ND	ND	ND
Decker Island					
Fall 2011	October 24 – November 30, 2011	0.1	0.6	13.8	23.3
Winter	December 1, 2011 – February 28, 2012	0.2	1.3	9.5	13.8
Spring	March 1 – May 30, 2012	0.1	0.5	14.1	23.7
Summer	June 1 – August 30, 2012	0.05	0.7	22.6	30.0
Fall	September 1 – November 30, 2012	0.2	1.8	18.7	26.2

Data were derived from 2-hour averages of 15-minute intervals

ND represents periods where no data were available

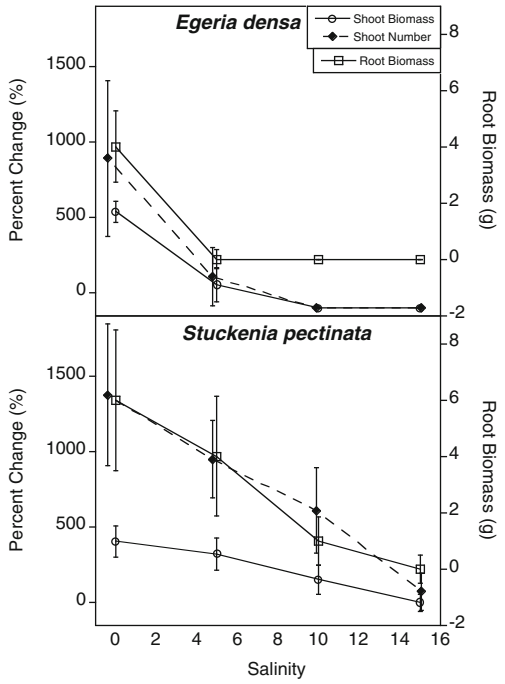

Fig. 2 Percent change in dry biomass and shoot number, and average root biomass for *E. densa* (*top*) and *S. pectinata* (*bottom*) grown in monoculture. *Error bars* represent 95 % confidence intervals (n = 5). Percent change in biomass and average root biomass are offset on the x-axis by −0.5 to display error bars clearly

Temperature and Salinity Experiment on *E. densa*

When considering all rounds of the temperature experiment together, there was a significant interaction between salinity and temperature on *E. densa* wet biomass, shoot length, and root length (all ANOVA and SRH tests, $p < 0.001$; Fig. 5), owing to higher salinities strengthening negative effects of increasing temperature. Within each of the 0, 5, and 10 salinity levels, increasing temperatures negatively affected *E. densa* growth, with greatest reductions in the 30 °C treatment, especially at salinities of 5 and 10 (Fig. 5). No roots were produced at a salinity of 10, regardless of temperature, even though aboveground biomass was present. At a salinity of 15, all plant tissue at all temperatures died and decomposed (Fig. 5).

Results of the control experiment were visually compared to those of the salinity level of 5 from the three experimental rounds conducted at a single temperature. Although the magnitude of effects was larger in the temperature experiment compared to the control experiment, response patterns for both experiments were very similar (Fig. 6). Change in wet biomass in the control experiment demonstrated the same significant difference by temperature as in the separate rounds of the temperature experiment ($p < 0.001$ for both; Fig. 6). Root length also produced similar trends in the control experiment as in the separate temperature rounds ($p = 0.01$; Fig. 6). We interpret this similarity in patterns as support that the separately run rounds of the temperature experiment can be considered together as one experiment as described in the previous paragraph.

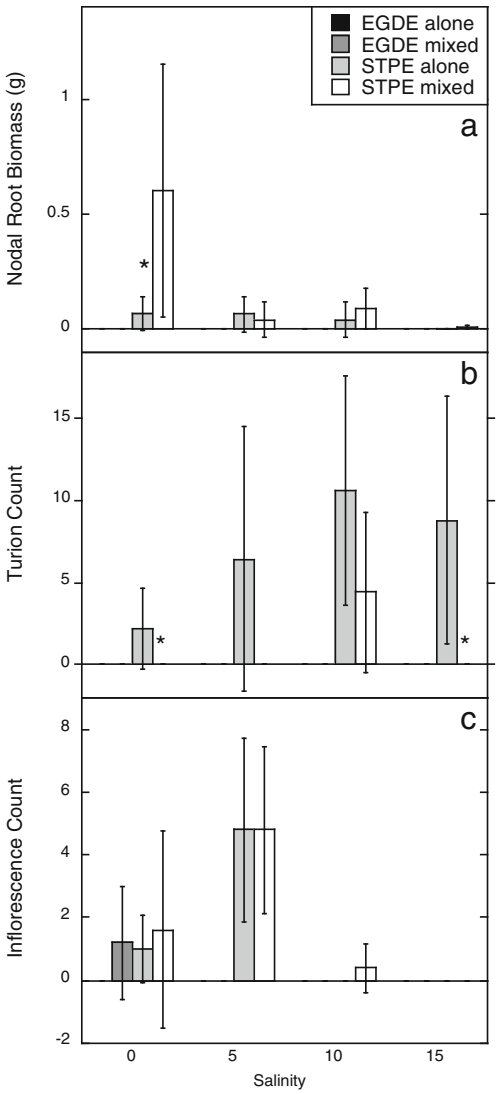

Fig. 3 Nodal root biomass (**a**), turion count (**b**), and inflorescence count (**c**) per tank. *Asterisks* denote significant differences between mixed- and monocultures for *E. densa* (EGDE) and *S. pectinata* (STPE). *Errors bars* represent 95 % confidence intervals (n = 5)

Discussion

Abundance of the native pondweed, *S. pectinata*, declines as salinities drop to near 0 in the upper San Francisco Estuary, concomitant with the occurrence of increasingly dense stands of the invader *E. densa* (Borgnis 2013). Competition can lead to exclusion of stress tolerant species from more benign abiotic conditions in tidal marshes (Crain et al. 2004) and other marine systems (Connell 1972; Paine 1974), but this possibility had not been considered in the Estuary's SAV distributions. We have provided evidence that *E. densa* is limited to the Estuary's fresh waters because it cannot endure higher

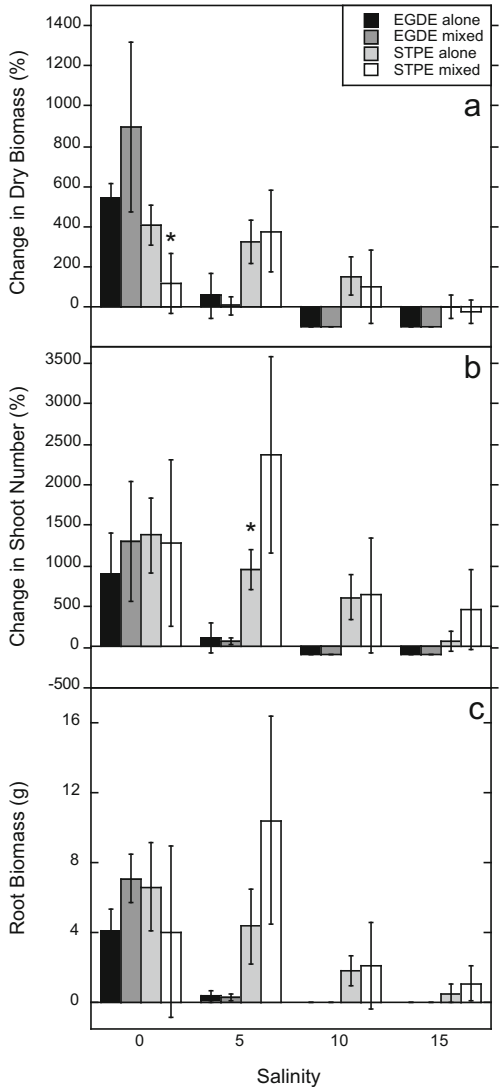

Fig. 4 Percent change in dry biomass (**a**) and shoot number (**b**), and final root biomass (**c**), for all salinity and vegetation treatments. *Species abbreviations*, *asterisks*, and *error bars* as in Fig. 3

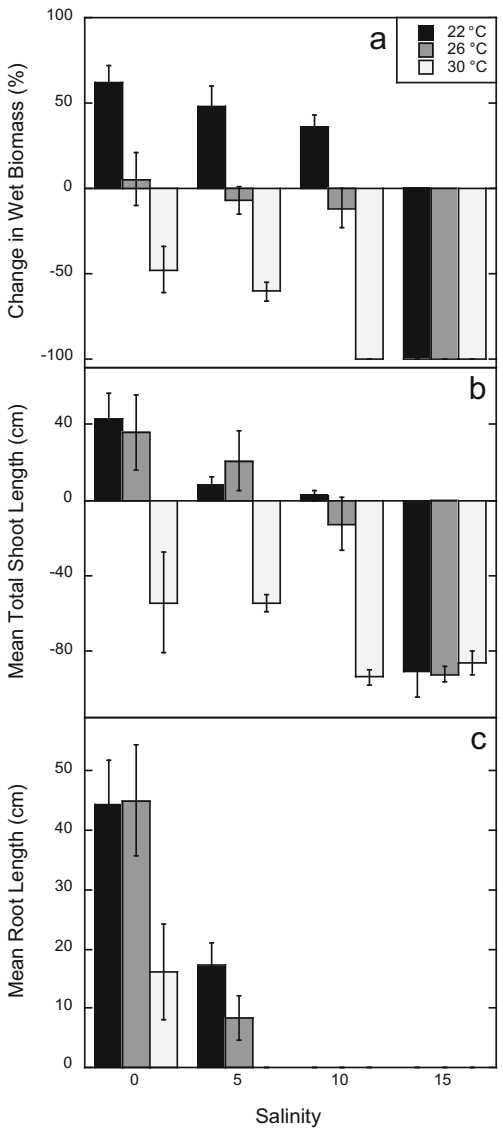

Fig. 5 Percent change in aboveground biomass (**a**) and shoot length (**b**), and average root length (**c**) for *E. densa* grown at 22, 26, and 30 °C. *Error bars* represent 95 % confidence intervals

salinities, with signs of severe stress at a salinity of 5 and complete mortality at 10 or 15. In contrast, *S. pectinata* tolerates brackish waters and would probably be more abundant in fresh waters were it not for competition with *E. densa*. These findings have implications for management of the invader and for expectations of submerged vegetation composition under future scenarios of water management and climate change.

S. pectinata was highly productive at salinities of 0 and 5, increasing fourfold in biomass and tenfold in shoot number, and with substantial increases in root production over 12 weeks. Although *S. pectinata* was less productive at a salinity of 10, it was able to double in biomass and increase sixfold in shoot number. Even at a salinity of 15, *S. pectinata* survived, with senescence followed by regrowth to initial biomass levels within the second month of the experiment. Notably, at a salinity of 5, aboveground biomass did not decline as inflorescence production increased, as has been observed for other aquatic plants (Van Zandt et al. 2003), suggesting that conditions did not result in a stress-related tradeoff between vegetative and reproductive allocation. There was no flowering at higher salinities (10 and 15); thus, a salinity of 5 may maximize both growth and reproductive potential. Similarly, a previous study found that a salinity of 3 favored tuber production, and although *S. pectinata* could still grow at a salinity of 12, a salinity of 15 reduced production or proved fatal for many plants (Teeter et al. 1965).

Clearly, *S. pectinata* can grow well at low salinities, and our data suggest that its current limited distribution in the fresher waters of the Delta relates in part to the presence of *E. densa*. Given that biomass accumulation was ~70 % lower and significantly fewer turions were produced in the presence

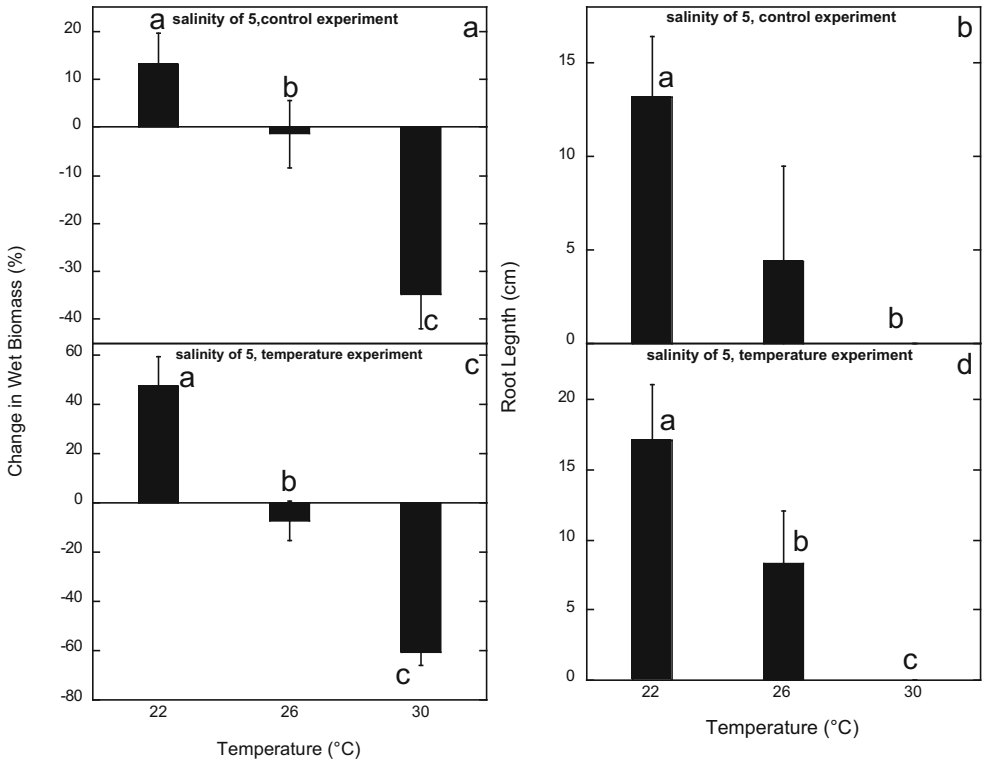

Fig. 6 Percent change in wet biomass (%) for *E. densa* in the control experiment in which all temperatures were held at a salinity of 5 (**a**) and the salinity level of 5 from the temperature experiment (**c**). Average root length (cm) for *E. densa* in the control experiment (**b**) and the salinity level of 5 from the temperature experiment (**d**). *Error bars* represent 95 % confidence intervals ($n = 5$). *Letters* denote significant differences in temperature treatments. Note the difference in scale on *y*-axis

of *E. densa*, *S. pectinata* may have limited potential for establishment and overwintering where *E. densa* co-occurs in fresh waters. Notably, it was this 0 salinity, mixed culture treatment that led to the highest production of adventitious roots at the leaf nodes (nodal roots) of *S. pectinata*, suggesting a foraging response under limited resource conditions (Keddy et al. 1998). Nodal root production in *S. pectinata* has been documented following an artificial addition of the plant hormone ethylene (Summers and Jackson 1998). Because ethylene typically "informs" SAV of submergence (Jackson 1990; Summers and Jackson 1998), this nodal root production may have been linked to resource deficiencies typically exaggerated by depth but in this case resulting from the vigorous growth response of *E. densa* in the freshwater mixed culture. Consistent with our findings, *E. densa* has been found to outcompete native SAV species in other freshwater zones of estuaries around the world (Wells et al. 1997; Hofstra et al. 1999; Hussner and Lösch 2005; Thiebaut 2007). Historic data are not available for the SFE, but considering the strong competitive abilities of *E. densa*, it is plausible that *S. pectinata* was more common in the Delta region prior to *E. densa* introduction.

The high abundance of *E. densa* in the Delta is likely supported by strong competitive abilities, but its advantage diminishes with increasing salinity. At a salinity of 5, *E. densa* biomass was greatly reduced and *S. pectinata* growth was enhanced in the mixed species treatment (as % change in shoot number and root biomass) over the monoculture. Although *E. densa* could not compete per se at higher salinities (where it did not survive), *S. pectinata* production of fewer turions at high salinities in mixed culture relative to monoculture suggests relict negative effects of *E. densa* presence. It may be that allelopathy is responsible for this result, as has been suggested by studies with phytoplankton (Vanderstukken et al. 2011). We cannot be certain of the mechanism, but it is intriguing that *E. densa*'s negative effects on *S. pectinata* occurred whether or not it survived.

Another potential stressor, temperature, was also important to *E. densa* abundance in our study. Experimental temperatures maintained at 22 °C, comparable to the highest average seasonal temperatures at all eight sites in Suisun Bay and the Delta during our study (21 to 23 °C), were very favorable for growth of *E. densa* fragments in freshwater. However, we found that a sustained increase of 4 °C or more was detrimental to *E. densa* biomass at all salinities. Although Barko and Smart (1981) found that temperatures up to 28 °C stimulated *E. densa* productivity in MS, USA, our results are concordant with those of a Japanese study in which *E. densa* growth was much reduced at temperatures higher than 21 °C (Haramoto and Ikusima 1988).

Expectations Under Future Conditions

While *E. densa* is dominant throughout the Delta now, our data suggest that rising salinity, resulting from sea level rise or management actions (see Introduction), will force *E. densa* to shift its distribution up-estuary in order to escape osmotic stress. Interestingly, temperature increases, which could be

exaggerated in already warmer inland areas, may present an opposing gradient of favorable conditions, thus squeezing *E. densa* into a limited space where both salinity and temperature remain low enough.

In contrast, *S. pectinata* appears to possess the physiological scope to withstand an average salinity increase of 5 and thus may be able to maintain its current distribution within Suisun Bay and the west Delta under increased salinity conditions. We were not able to test temperature effects on *S. pectinata*, but other studies have found it is able to withstand temperatures up to 37 °C (Barko and Smart 1981; Spencer and Anderson 1986; Pilon and Santamaria 2002); with this high temperature tolerance, *S. pectinata* may be better suited than *E. densa* for increased temperature conditions predicted with climate change.

Our finding that *E. densa* presence leads to large declines in *S. pectinata* biomass in freshwater conditions suggests that increased salinity in the Delta would allow additional space for *S. pectinata* as *E. densa* dies back and can no longer maintain competitive exclusion. Hence, we predict that overall acreage of *S. pectinata* will increase in the future due to persistence within its current distribution as described above as well as expansion into areas where *E. densa* is currently dominant. That *E. densa* may restrict *S. pectinata* from fresher areas also suggests that management of the invader (e.g., through applying herbicides as is done by the CA Department of Parks and Recreation Division of Boating and Waterways in areas of the central Delta; Johnson et al. 2006; Becerra 2011) could lead to greater acreage of *S. pectinata*, perhaps enhanced with active restoration of the native. To better predict future distributions and conserve habitat provided by native SAV, additional experimentation and continued field surveys are needed to understand species interactions and multi-stressor effects.

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