An Inexpensive Method to Identify the Elevation of Tidally Inundated Habitat in Coastal Wetlands

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Abstract.—We explored the use of an inexpensive "vial" method to measure the elevations reached by a series of high tides, which included the highest tides of the year, at sites in four southern California wetlands, examined variation in the distribution and abundance of marsh, transition, and upland vegetation as a function of elevation, and assessed whether our measure of height of tidal inundation correlated with the distribution of these plants, permitting the use of vegetation boundaries as a proxy for the height of tidal inundation. The potential effects of factors unrelated to tidal inundation render elevational boundaries of native marsh plants unattractive as a general criterion for defining the upper edge of tidally influenced habitat. By contrast, both the upper limit of tidal inundation as measured by the vial method and the lower elevational limit of exotic grasses, such as Parapholis incurva, appears to be useful in delineating the upper edge of tidally influenced habitat. This elevation coincided with the highest spring tides and varied among sites in association with the extent of tidal muting. The vial method is a useful technique to identify sites of comparable tidal influence in restored and reference wetlands and can provide an early indication of tidal muting in restored wetlands.

The performance of restoration projects in tidal wetlands has been assessed using several methods (reviewed in Kentula 2000). One approach is to compare the degree of similarity of the restored site, in terms of selected physical and biological criteria, to natural reference wetlands. For tidal wetlands, a definition of "tidally-influenced" habitat may first be needed to delineate the general area for comparison across sites. Physical criteria used to define "tidally influenced"

habitat are ambiguous, but may include that the "substrate is at least irregularly exposed and flooded by oceanic tides" (Ferren et al. 1996abc). Tidal wetland soils are characterized by low permeability and halophytic vegetation (e.g., *Salicornia, Spartina*) may be present.

Unfortunately, these definitions are subject to interpretation. Tidal influence can be defined statistically as a greater than zero probability of inundation by tidal waters. In practice, such a definition could include habitats that are inundated by tidal waters much less frequently than even once per year (e.g., once every five or ten years). Such a definition does not consider that ecological functioning may vary greatly as a function of inundation frequency; habitat at the upper end of the tidal gradient may function differently relative to habitats lower (e.g., be more susceptible to invasion by exotic species). Similar problems occur when using the presence of hydric soils or halophytic plants to define tidally influenced habitat, since both can occur in seasonal wetlands far removed from tidal influence (Ferren et al. 1996a).

In addition, the biological structure and function of the restored site may be compared to those characteristics in control or reference sites in "equivalent" tidally influenced habitats. Elevation *per se* is only an approximate measure of tidal influence or the frequency of tidal inundation because local hydrology and soil characteristics may influence the relationship between these variables (Van Der Molen 1997). To permit comparisons of habitats characterized by similar inundation regimes, it is necessary to examine the relationship between elevation and inundation in wetlands. Unfortunately, this comparison can require use of expensive instruments, thereby limiting the number of sites that can be simultaneously measured.

The distribution and abundance of plant species may also be used to characterize "equivalent" habitats. The distribution and abundance of marsh plants and the lower limits of transition and upland plants vary as a function of elevation and, by inference, frequency of tidal inundation (e.g., Zedler 1977; Callaway et al. 1990; Bertness 1991ab; Pennings and Callaway 1992; Zedler et al. 1999). Despite the existence of numerous studies on the distribution of plants in salt marshes, however, little published information is available on how plant distributions may be related to the height of tidal inundation; information that could prove useful in the development of criteria to define "tidally influenced" habitat and in choosing "equivalent" habitats for comparisons across restored and reference wetlands. Previous work has suggested that the elevational limits of marsh plants may vary among estuaries even within the same region (Frenkel et al. 1981).

In this study, we explored the use of an inexpensive technique to measure the elevations reached by a series of high tides, which included the highest tides of the year, at sites in four southern California wetlands. We examined whether our measure of height of tidal inundation correlated with the distribution and abundance of marsh, transition, and upland vegetation, thus permitting the use of vegetation boundaries as a proxy for the height of tidal inundation.

Materials and Methods

Study Sites

To examine relationships between elevation, the height of tidal inundation, and the distribution and abundance of vegetation, we collected data along transects at

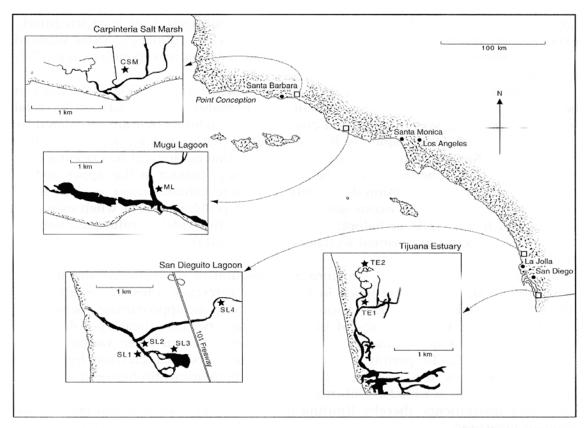


Fig. 1. Map showing location of study sites at San Dieguito Lagoon, Carpinteria Salt Marsh, Tijuana Estuary, and Mugu Lagoon. Tide data from the open coast measured at Santa Monica and La Jolla and reported by the National Oceanic and Atmospheric Administration (see text). Inset maps modified from Ferren (1985), Onuf (1987), SAIC (2000), and Zedler et al. (1992).

8 sites distributed among 4 wetlands (San Dieguito Lagoon, Tijuana Estuary, Carpinteria Salt Marsh, and Mugu Lagoon) that incorporated a range of inundation regimes. Four sites were located at varying distances from the ocean inlet in San Dieguito Lagoon (32°58′N, -117°08′W) (Fig. 1). This wetland, located at the northern edge of the City of Del Mar, consists of ~61 ha of estuarine habitat, including 25 ha of tidal salt marsh (SAIC 2000) (Fig. 1). The western portion of the estuary consists of salt marsh with tidal channels 15 m to 30 m wide and one 28 ha basin. The eastern portion of the estuary consists of the San Dieguito River channel with a narrow strip of salt marsh along the southern border of the river. Three sites (SL1, SL2, SL3) were located in the western portion of the estuary at distances of ~1.4, 1.3, and 1.9 km, respectively from the inlet. One site (SL4) was located in the eastern portion ~2.6 km from the inlet. Two transects spaced ~2 m apart were established at each site perpendicular to tidal channels (SL1, SL2, SL4) or a basin (SL3).

Tidal exchange in San Dieguito Lagoon occurs through an inlet to the Pacific Ocean. Sand accretion can block the inlet preventing tidal exchange. For example, between March 1992 and May 1993 the inlet was closed (MEC 1993). However, the inlet was estimated to have been open 90% of the time from October 1994 through September 1997 (Boland 1998).

Two sites (TE1, TE2) were sampled in Tijuana Estuary (32°33′N, -117°05′W), located in the southwestern corner of San Diego County. Tijuana Estuary encompasses ~712 ha of wetland habitat, including ~249 ha of tidal salt marsh. The ocean inlet is generally open but is relatively shallow, which could reduce tidal exchange in this estuary (Zedler et al. 1992). One transect was established at each site, which extended perpendicular to the edge of 1 to 2 m wide tidal creeks located ~1.6 km (TE1) and 2.2 km (TE2) from the inlet (Fig. 1).

One site (CM) was located in the eastern portion of Carpinteria Salt Marsh (34°24′N-119°31′W). This marsh contains ~93 ha of wetland habitat, including ~54 ha of tidal salt marsh (Ferren 1985; Page et al. 1995). Tidal exchange occurs year round through the inlet that is flanked by rock revetments. However, total tidal range and the tidal prism are reduced due to a cobble sill at the inlet (Hubbard 1996). One transect was established perpendicular to the edge of a small (1 m wide) tidal creek ~0.9 km from the inlet (Fig. 1).

The last site (ML) was located east of the central basin at Mugu Lagoon (34°06′N-119°05′W). Mugu Lagoon contains ~597 ha of wetland habitat, including ~382 ha of tidal salt marsh (Onuf 1987). The lagoon consists of a western arm, an eastern arm, and a central basin section. The inlet/barrier beach varies dynamically with fluvial and nearshore processes, but the inlet is continuously open to tidal exchange. One transect was run perpendicularly from the edge of a 5 m wide tidal channel approximately 1.0 km from the inlet (Fig. 1).

Transects extended from the nonvegetated waters edge into upland vegetation. Consequently, transect length varied depending on the elevational slope at each site (i.e. <30 m at SL1 and SL4 to >200 m at ML, CM, and TE1). Measurements of elevation, plant species composition and percent cover were taken at stations located at uniform distances along each transect. Stations along the transects were generally spaced 10 m apart except at sites SL1 and SL4, where stations were spaced 2 m apart because of the relatively short length of these transects. It should be noted that data on elevation, tidal inundation, and vegetation from our study sites were collected for the purpose of examining relationships among these variables rather than to fully characterize these variables for each wetland.

Measurements of Tidal Elevation and Height of Tidal Inundation

Elevations were determined at every station along each transect using a differential GPS system (Sokkia RTK Receiver System) in October 1998. To determine the repeatability of these measurements, the elevation of 25 stations at San Dieguito Lagoon were remeasured in January 1999. Measurements of elevation in January were similar to those determined in October, differing on average by 2.1 cm (range 0 to 4.8 cm) from the previous measurements. All elevations are expressed relative to NGVD (National Geodetic Vertical Datum = Mean Sea Level in 1929). Current mean sea level (MSL) is 0.017 m NGVD.

We explored the use of an inexpensive "vial" method to measure the elevations reached by a series of high tides between November 1997 and March 1998 at each site. This series included the highest tides of the year. We placed a vertical stake at or near the beginning of each transect at a known elevation. Glass 20 ml vials were attached to each stake at 3 cm intervals. The elevation reached by a given high tide in the marsh was measured by noting the elevation of the highest vial on the stake that was filled with seawater. Vials were emptied prior to each

measured high tide. Our measurements presumably correlated with inundation frequency and submersion time for a given elevation and thus provided a comparative measure of the inundation environment at each site.

Using the vial measurements, we determined the degree of muting of the high tides at the study sites relative to tides on the coast. High tides in San Dieguito Lagoon and Tijuana Estuary were compared with the same high tides at La Jolla (Scripps Pier), as reported by the National Oceanic and Atmospheric Administration (NOAA). San Dieguito Lagoon and Tijuana Estuary are located 11 km south and 37 km north of La Jolla, respectively (Fig. 1). The elevations reached by high tides at Mugu Lagoon and Carpinteria Salt Marsh were compared with the same high tides observed at Santa Monica (NOAA). Mugu Lagoon and Carpinteria Salt Marsh are located 60 km and 120 km north of Santa Monica, respectively (Fig. 1).

Vegetation Sampling

We identified and measured the percent cover of plant species along the transects at each site. Percent cover was determined using point-contact sampling. A 4 mm diameter rod was dropped through 25 randomly placed holes in a sampling table situated above a 0.5 m × 0.5 m quadrat at each station along the transect lines. All species touching the rod were recorded and the percent cover of each plant species was determined by multiplying the number of contacts by four. Because more than one species could contact the rod, the total cover can exceed 100%. Following quantitative sampling, each quadrat was searched and any additional species encountered were recorded as covering <4%. Although we collected data on all marsh plant species, here we present only data on the most ubiquitous species (the native succulents Salicornia virginica and Arthrocnemum subterminale, the invasive grass, Parapholis incurva, and a grouping of transition/ upland species that included the native rush, Juncus bufonius, non-native grasses Polypogon monspeliensis, Lolium multiflorum, Bromus diandrus, and B. hordeaceus, the native shrubs Isocoma mensiezii, Lycium californicum, Rhus integrifolia, and the weeds *Brassica* sp. and *Gnathophalium* sp).

Data Analyses

All statistical analyses were done using Systat Version 8.0 (SPSS Inc. 1998). Linear regressions of the elevation reached by high tides on the stakes against the elevations reached by high tides on the coast were compared among sites using Analysis of Covariance (ANCOVA) to determine whether the degree of muting varied among sites. In this analysis, site was the categorical variable with elevation as the covariate. We used multiple regression analysis to evaluate relationships between the lower elevational limits of Arthrocnemum subterminale, Parapholis incurva, and grouped transition/upland species, and the independent variables of tidal muting and marsh slope. The upper limits of distribution of these plants were not considered in this analysis because these species occur in non-tidal habitats. Tidal muting at the lower limits of plant species was calculated from the regression equation that described the relationship between the elevations reached by high tides at each site and along the open coast at La Jolla or Santa Monica. Slope was calculated as the average change in elevation over a distance of 10 m (the typical distance between stations) from the lower limit for each plant group towards the creek, channel or basin.

Results

Site Elevations and Marsh Topography

Elevation and marsh topography varied among sites (Fig. 2). As expected, elevation was highly correlated with distance from tidal creek, channel, or basin for all transects (P < 0.001 for SL1, 3, 4, ML, CM, TE1, TE2; P < 0.01 for SL2). However, the marsh plain (sensu Zedler et al. 1999) occurred at higher elevations (>0.75 m NGVD) at SL1, 2, 3, 4, and ML compared with CM, TE1 and TE2. The marsh plain at CM and ML had a uniform, gradual slope while the elevation of TE1 varied primarily at distances of 160 to 240 m from the channel. TE2 crossed irregular topography that included a low nonvegetated area 60 m from the channel. The elevations of SL1, 2, and 4 varied primarily at the channel and upland ends of the transects. Much of SL3 covered elevations >1.5 m with abrupt changes in elevation at the basin and upland ends of the transect.

Elevation of High Tides

As expected, there was a linear relationship between the elevation reached by high tides at each site and high tides measured along the open coast (Fig. 3). However, vial measurements of tidal inundation indicated that high tides were muted at 7 of the 8 sites. Within San Dieguito Lagoon, high tides were from 0.06 to 0.09 m lower at SL1, 2, and 3 compared with those measured on the open coast. Because there was no difference between these sites (P > 0.05, ANCOVA), the data are grouped in Figure 3. In contrast, high tides at SL4, the most landward site, reached higher elevations than those measured on the open coast. This "run-up" effect appeared to increase with height of the high tide. For example, from the regression equation for SL4, a high tide of 1.8 m on the open coast would yield a tide of 2.0 m at this site (Fig. 3). High tides were also from 0.06 to 0.09 m lower at ML compared with those measured on the open coast. Because there was no difference between ML and SL1, 2, and 3 (P > 0.05, ANCOVA), the data from ML are grouped with the latter sites in Figure 3.

The greatest muting of tides occurred at CM, TE1, and TE2; high tides at these sites were ~ 0.3 m lower than the same tides along the open coast. There was no difference in tidal muting between CM, TE1, and TE2 (P > 0.05, ANCOVA) and the data from these sites are grouped in Figure 3.

Plant Species Distributions and Elevation

There was broad overlap in the distribution of *Salicornia virginica* and *Arthrocnemum subterminale*. However, as expected (Zedler et al. 1992; Pennings and Callaway 1992), the highest cover of these species occurred at different elevations; highest cover of *S. virginica*, occurred consistently at lower elevations than the highest cover of *A. subterminale* (Fig. 4). However, across sites, the highest cover of these species generally varied with the degree of tidal muting (Fig. 4). For example, highest cover of *S. virginica* (to 100%) occurred at elevations of >0.60 m NGVD at the least muted sites (SL1, 2, 3, and ML), but was virtually absent at elevations of >0.60 m NGVD at the most muted sites (CM, TE1, and TE2). Similarly, highest cover of *A. subterminale* occurred at elevations occupied by transition/upland plants at the most muted sites (Figs. 4, 5). At the site of tidal "run-up" (SL4), *S. virginica* also occurred at elevations of >0.60 m

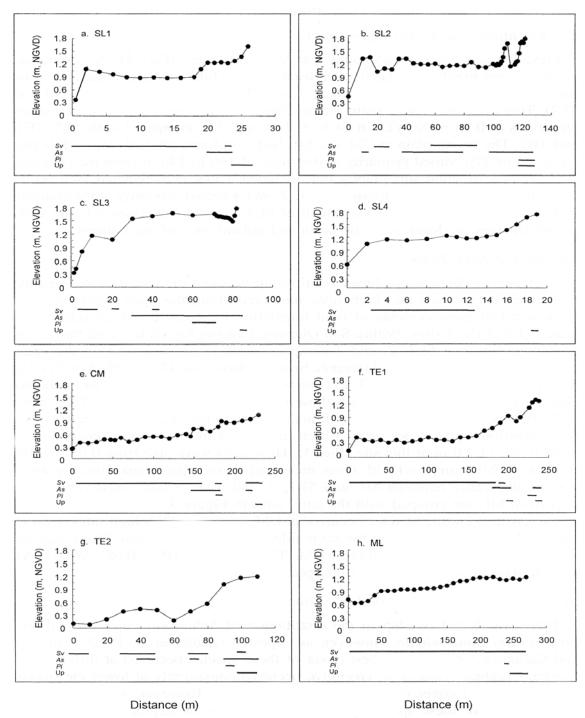


Fig. 2. Profiles of elevation (m, NGVD) versus distance from channel/basin at sites in San Dieguito Lagoon (SL1, 2, 3, 4), Carpinteria Salt Marsh (CM), Tijuana Estuary (TE1, 2), and Mugu Lagoon (ML), and the distribution of *Salicornia virginica*, *Arthrocnemum subterminale*, *Parapholis incurva*, and grouped upland plants along transects. Values from means of two transects at SL1, 2, 3, and 4 and from one transect at CM, TE1, 2, and ML. Note that the scale of the x-axis varies among sites. Plant abbreviations: *Sv—Salicornia virginica*, *As—Arthrocnemum subterminale*, *Pi—Parapholis incurva*, Up—transition/upland group.

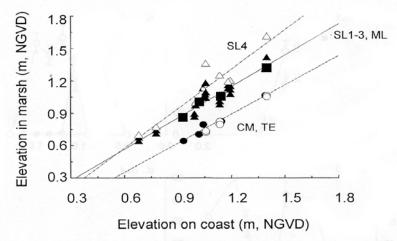


Fig. 3. Linear regressions of the elevation of high tides measured at the wetland study sites against the elevation of high tides measured on the open coast on the same date. Elevations at San Dieguito Lagoon (SL) and Tijuana Estuary (TE) are compared with elevations at Scripps Pier. Elevations at Carpinteria Salt Marsh (CM) and Mugu Lagoon (ML) are compared with elevations at Santa Monica. Each point represents one high tide. Common regression line —— computed for SL1-3 (\blacktriangle) and ML (\blacksquare): y = 0.97x - 0.06, $r^2 = 0.89$, n = 27; SL4 ----- (Δ): y = 1.22x - 0.52, $r^2 = 0.88$, n = 8. Common regression line —— for CM (\blacksquare) and TE (\bigcirc): y = 0.91x - 0.70, $r^2 = 0.98$, n = 12.

NGVD, but was not abundant (cover <20%) and A. subterminale was absent. Jaumea carnosa was the most abundant plant at this site (unpubl. data). At two sites (SL2, SL3), A. subterminale occurred at elevations (1.95 m NGVD) above the highest observed water level reported along the coast (1.5 m NGVD, August 8, 1983) (Fig. 4).

There were also differences in the lower limits of distribution of transitional and upland species among sites having different degrees of tidal muting. For example, the lower limit of the invasive grass, *Parapholis incurva*, occurred on average ~ 0.54 m lower at the sites of greatest tidal muting (CM, TE1, and TE2) (Fig. 5). The lower limit of plants grouped in the transition/upland category occurred 0.75 m lower at CM compared with SL4. These species were present in high cover (70–100%) at CM, TE1, and TE2 at elevations (0.90–1.20 m NGVD) occupied entirely by marsh plants at SL1, 2, 3 and 4. The lower limits of *Parapholis incurva* and transition/upland plants at the different sites were significantly correlated with the elevation reached by the highest high tide measured in this study (3 December 1998, third highest tide of 1998 at La Jolla with an observed high of 1.41 m, *P. incurva*, P < 0.01, r = 0.95, df = 4; transition/upland: P < 0.001, r = 0.95, df = 6: Fig. 6).

Relationship between the Lower Limit of Vegetation, Tidal Muting, and Marsh Slope

Tidal muting explained a significant amount of variation in the lower limits of *Parapholis incurva* and the transition/upland group, but not in *Arthrocnemum subterminale* (Table 1). In contrast, marsh slope did not explain any significant variation in the lower limits of any of the species studied.

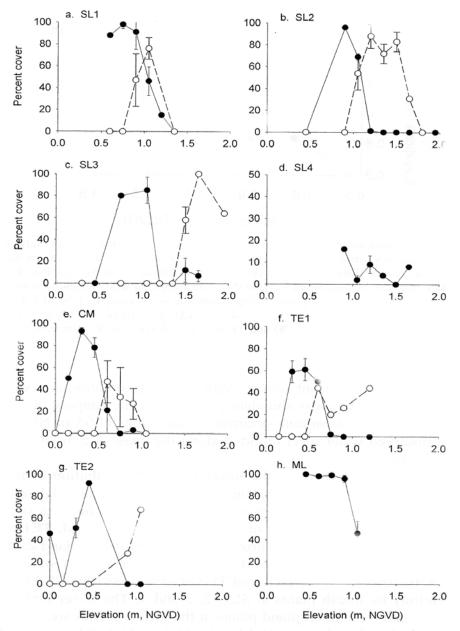


Fig. 4. Percent cover versus elevation (m, NGVD) for Salicornia virginica (●) and Arthrocnemum subterminale (○). Data grouped in 0.15 m elevation classes. Mean values ±1SE. Standard errors are shown only when number of quadrats >2. Note that the y-axis of (d) extends only to 50% cover. A. subterminale absent from SL4 (d) and ML (h).

Discussion

Our study was motivated by the desire to identify similar tidally influenced habitats at different wetland sites on the basis of elevation, height of inundation, and/or vegetation. We used an inexpensive vial method to characterize sites in terms of height of tidal inundation and examined whether plant distribution and cover were similar for equivalent heights of inundation.

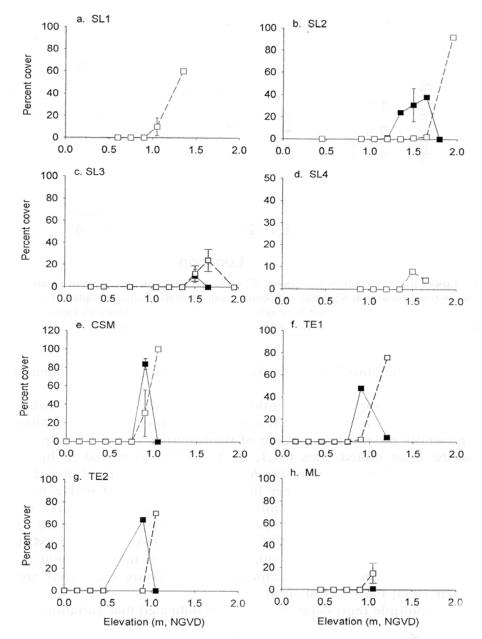


Fig. 5. Percent cover versus elevation (m, NGVD) for *Parapholis incurva* (■) and grouped transitional/upland plants (□). Data grouped in 0.15 m elevation classes. Mean values ±1SE. Standard errors are shown only when number of quadrats >2. Note that the y-axis of (d) extends only to 50% cover. *P incurva* absent from SL1 (a) and SL 4 (d).

The relationship between elevation and height of tidal inundation varied among sites making elevation *per se* unattractive as a general criterion for delineating "tidally influenced" habitat. High tides were muted relative to coastal high tides at all but one site (SL4). The specific reasons for the differences in tidal muting among sites are not known, but channel morphology may be a contributing factor (e.g., Van der Molen 1997). Transects at Tijuana Estuary and Carpinteria Salt Marsh ran perpendicular to small tidal creeks (<1 m wide) while transects at

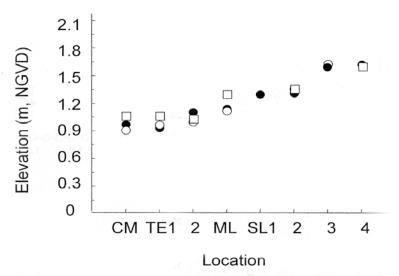


Fig. 6. Lower limit of *Parapholis incurva* (\bigcirc) and grouped transition/upland plants (\bigcirc) at study sites. *P. incurva* not present at SL1 and 4. Species grouped in the transition/upland category given in text. Elevation reached by the highest high tide measured during this study (3 December 1998) also plotted (\square). No tidal height data are available from SL1 and SL3 on this date.

Mugu and San Dieguito Lagoons originated off wider, deeper channels (>5 m wide) (or a basin).

The elevational range of distribution of *Salicornia virginica, Arthrocnemum subterminale* (absent at SL4 and ML), *Parapholis incurva*, and transition/upland species generally reflected the degree of tidal muting across sites. Indeed, marsh plants at the least muted sites (SL1, 2, 3, 4, ML) occurred in high cover at elevations occupied only by transition/upland plants at the most muted sites (CM, TE1, TE2). As expected, the upper limit of distribution of native marsh plants was not useful in defining tidally influenced habitat; *A. subterminale* occurred at or above (SL3, Fig. 4, Page, unpublished data) the highest observed tidal water level of 2.3 m NGVD measured at Scripp's Pier on 8 August 1983 (MEC, 1993). *A. subterminale, S. virginica,* and other marsh plants may be found in nontidal habitats (seasonal marsh) if soil salinities and moisture conditions are suitable (e.g., Ferren 1985; Ferren et al. 1996c).

Results of multiple regression analysis also indicated that variation in the lower

Table 1. Summary of the results of multiple regression analysis evaluating the relationship between the lower elevation limit of *Arthrocnemum subterminale*, *Parapholis incurva*, a grouping of transition/upland plant, and marsh slope and tidal muting.

Effect	$Arthrocnemum \\ subterminale \\ (n = 6)$				Parapholis incurva (n = 5)				Transition/upland plants $(n = 8)$			
	Coeff	Std	t svi	P	Coeff	Std	esbii t	P	Coeff	Std error	nfluen ohe s	P
Constant	0.83	0.24	3.51	0.039	1.73	0.09	19.11	0.003	1.40	0.08	17.67	< 0.001
Slope	3.84	2.02	1.90	0.154	0.51	0.23	2.27	0.151	0.17	0.39	0.43	0.685
Muting	0.28	0.30	0.93	0.423	2.53	0.11	6.91	0.020	0.39	0.12	3.69	0.014

limit of Arthrocnemum subterminale could not be accounted for simply in terms of tidal muting and marsh slope (Table 1). Biological interactions (Pennings and Callaway 1992) and disturbance (Callaway and Pennings 1998) may obscure relationships between tidal muting and the lower limit of this species. For example, competition between A. subterminale and Salicornia virginica can affect the location of the boundary of both species (Pennings and Callaway 1992). A. subterminale has a greater tolerance of high soil salinity, allowing this species to exist high in the marsh while S. virginica has a greater tolerance of inundation, allowing this species to exist lower in the marsh. In areas where both species overlap, small differences in soil salinity and moisture over short distances may modify the outcome of competitive interactions between these species (Pennings and Callaway 1992).

The lower elevational limits of *Parapholis incurva* and transition/upland species were correlated with variation in the degree of tidal muting across sites (Table 1) and with the elevation reached by the highest tide (1.4 m NGVD at La Jolla). *P. incurva* and other transition or upland plants are sensitive to elevated soil salinities, which probably limits these species from occurring at lower elevations (Callaway and Sabraw 1994; Kuhn and Zedler 1997; Callaway and Zedler 1998).

Exotic grasses such as *Parapholis incurva* and *Polypogon monspeliensis* are not desirable in restored marshes because they occupy space, preclude the establishment of native species, and may not provide the functions (e.g., food, shelter, nesting habitat) of native plants (Zedler 1996). Results from this study show that the lower elevational limit of such species may prove to be a useful proxy for delineating the upper edge of tidally influenced habitat. Below the lower limit of exotic grasses, the vial method is an effective and inexpensive technique that can be used to identify sites of comparable tidal influence in restored and reference wetlands.

Acknowledgements

We thank S. Anghera and M. Meeker for field assistance, T. Keeney and the U. S. Naval Air Station at Point Mugu for permission to work at Mugu Lagoon, and M. Pessino and J. Jones for Figure 1. We also thank D. Hubbard and J. Dugan for comments on the manuscript. Funding for this study was provided by Southern California Edison as required by the California Coastal Commission under SCE's coastal development permit (No.6-81-330-A, formerly 183-73) for Units 2 and 3 of the San Onofre Nuclear Generating Station.

Literature Cited

- Bertness, M. D. 1991a. Interspecific interactions among high marsh perennials in a New England salt marsh. Ecology, 72: 125–137.
- ——. 1991b. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. Ecology, 72: 138–148.
- Boland, J. M. 1998. Water quality monitoring of San Dieguito Lagoon. Final Report. California Coastal Commission, San Diego, California.
- Callaway, J. C., and J. B. Zedler. 1998. Interactions between a salt marsh native perennial (Salicornia virginica) and an exotic annual (Polypogoń monspeliensis) under varied salinity and hydroperiod. Wetland Ecology and Management, 5: 179–194.
- Callaway, R. M., and S. C. Pennings. 1998. Impact of a parasitic plant on the zonation of two salt marsh perennials. Oecologia, 114: 100–105.

- ———, and C. Sabraw. 1994. Effects of variable precipitation on the structure and diversity of a California salt marsh community. J. Veg. Sci., 5: 433–438.
- ———, S. Jones, W. R. Ferren, and A. Parikh. 1990. Ecology of a mediterranean-climate estuarine wetland at Carpinteria, California: plant distributions and soil salinity in the upper marsh. Can. J. Bot., 68: 1139–1146.
- Ferren, W. R., Jr. 1985. Carpinteria salt marsh: environment, history, and botanical resources of a southern California estuary. The Herbarium, Department of Biological Sciences, University of California, Santa Barbara, CA. Publication No. 4.
- Ferren, W. R., Jr., P. L. Fielder, and R. A. Leidy. 1996a. History of wetland classification. Madroño, 43: 105–124.
- ———, K. D. Lafferty, and L. A. K. Mertes. 1996b. Classification and description of wetlands of the central and southern California coast and coastal watersheds. Madroño, 43: 125–182.
- ——. 1996c. Key and catalogue of wetlands of the central and southern California coast and coastal watersheds. Madroño, 43: 183–233.
- Frenkel, R. E., H. P. Eilers, and C. A. Jefferson. 1981. Oregon coastal salt marsh upper limits and tidal datums. Estuaries, 4: 198–205.
- Hubbard, D. M., 1996. Tidal cycle distortion in Carpinteria Salt Marsh, California. Bull. So. Cal. Acad. Sci., 95: 88–98.
- Kentula, M. E. 2000. Perspectives on setting success criteria for wetland restoration. Ecological Engineering, 15: 199–209.
- Kuhn, N. L., and J. B. Zedler. 1997. Differential effects of salinity and soil saturation on native and exotic plants of a coastal salt marsh. Estuaries, 20: 391–403.
- MEC Analytical Systems. 1993. San Dieguito Lagoon Restoration Project Biological Baseline Study March 1992–May 1993. Volume 1. Prepared for Southern California Edison.
- Onuf, C. P. 1987. The ecology of Mugu Lagoon, California: An estuarine profile. U.S. Fish and Wildlife Report 85, 122 p.
- Page, H. M., R. L. Petty, and D. E. Meade. 1995. Influence of watershed runoff on nutrient dynamics in a southern California salt marsh. Est. Coastal Shelf Sci., 41: 163–180.
- Pennings, S. C., and R. M. Callaway. 1992. Salt marsh plant zonation: The relative importance of competition and physical factors. Ecology, 73: 681–690.
- SAIC. 2000. Environmental Impact Report/Environmental Impact Statement (EIR/EIS) for the San Dieguito Wetland Restoration Project. Draft Report prepared for the U.S. Fish and Wildlife (USFWS) and the San Dieguito River Park Joint Powers Authority (JPA), 646 pp.
- Van Der Molen, J. 1997. Tidal distortion and spatial differences in surface flooding characteristics in a salt marsh: implications for sea-level reconstruction. Est. Coastal Shelf Sci. 45: 221–233.
- Zelder, J. 1977. Salt marsh community structure in the Tijuana estuary, California. Est. Coastal Marine Sci. 5: 39–53.
- Principal Author. 1996. Tidal Wetland Restoration: A Scientific Perspective and Southern California Focus. California Sea Grant College System, University of California, La Jolla. Report No. T-038.
- ———, C. S. Nordby, and B. E. Kus. 1992. The ecology of Tijuana Estuary, California: a national estuarine research reserve. NOAA Office of Coastal Resource Management, Sanctuaries and Reserves Division, Washington, D. C.
- ——, J. C. Callaway, J. S. Desmond, G. Vivian-Smith, G. D. Williams, G. Sullivan, A. E. Brewster, and B. K. Bradshaw. 1999. Californian salt-marsh vegetation: an improved model of spatial pattern. Ecosystems, 2: 19–35.
- Accepted for publication 12 December 2002.