Gastropod Colonization of a Created Coastal Wetland: Potential Influences of Habitat Suitability and Dispersal Ability

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Abstract

We investigated the assumption that populations of epibenthic macroinvertebrates readily establish in created coastal wetlands by quantifying the spatial and temporal patterns of *Cerithidea californica* (California horn snail) density in a newly created wetland and an adjacent natural area in Mugu Lagoon, southern California, United States, for 3.5 years. The natural and created sites differed in vascular plant cover and sediment grain size, organic content, salinity, and moisture content. Densities of *C. californica* in the created site changed little during the study period, and were often lower than those in the natural site. The influences of habitat suitability and dispersal limitation on *C. californica* colonization of the created site varied among snail age classes. Sediment moisture and organic content explained some of the variability in subadult (47%) and adult (55%) density and relative abundance, but none of the variability in juvenile abundance. Adult snail density was also strongly influenced by distance from the natural/created site transition zone. Juvenile and subadult snail densities were not related to distance from the natural site, possibly due to greater dispersal ability. Between-site differences in *C. californica* densities and size structure suggested that adult snails were affected by both habitat characteristics and dispersal ability, subadults were influenced to a lesser degree by habitat characteristics, and juveniles were not related to either factor. Accordingly, the influence of habitat characteristics and dispersal ability on created site colonization may change with snail age. Successful restoration of benthic invertebrate communities requires consideration of both habitat characteristics and dispersal ability of the target species, even in created sites in close proximity to natural areas.

Key words: ***Cerithidea californica*, colonization, dispersal, gastropods, ontogenetic shifts, wetland restoration.**

Introduction

Efforts to restore coastal wetlands often focus on plants or specific threatened species (Broome et al. 1988; Zedler 1993; Parsons & Zedler 1997; Powell & Collier 2000), and tacitly rely upon the "field of dreams" assumption: build it and they will come (Palmer et al. 1997; Block et al. 2001). However, studies that address invertebrate colonization of created habitats often reveal deficiencies in species diversity, richness, or abundance (Moy & Levin 1991; Sacco et al. 1994; Levin et al. 1996; Minello & Webb 1997; Posey et al. 1997; Zajac & Whitlatch 2001), although few of these studies have examined systems on the west coast of the United States (but see Scatolini & Zedler 1996; Talley & Levin 1999).

Explanations for differences between invertebrate populations in created and natural sites are frequently attributed to dispersal limitations. The field of dreams assumption may hold true for mobile organisms such as birds (Passell 2000) or fish (Williams & Zedler 1999), but organisms with restricted dispersal ability, such as some invertebrates, may not rapidly colonize created sites (Levin et al. 1996; Brown et al. 1997; Lehtinen & Galatowitsch 2001). Of particular concern in coastal wetlands are organisms that lack planktonic dispersal stages, including some oligochaetes, tanaids, and gastropods; these groups are among the slowest colonizers of created habitats (Race 1981; Levin et al. 1996). In addition, those species that require continuous habitat for dispersal along the benthos are likely to be limited when habitat is patchy or corridors between patches are small (Brown et al. 1997; Lehtinen & Galatowitsch 2001).

Poor habitat quality in created sites may also influence colonization by invertebrate populations. Although many wetland organisms are tolerant of a wide range of physical conditions (Kneib 1984), both biotic and abiotic characteristics often influence invertebrate distribution and ability to colonize new habitats (Levin & Talley 2000). Sediment organic content, for example, is often closely related to grain size and influences food availability for detritivores and other benthic consumers (Moy & Levin 1991; Sacco

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et al. 1994; Levin et al. 1996; Scatolini & Zedler 1996; Minello & Webb 1997; Evans et al. 1998; Talley & Levin 1999; Zajac & Whitlatch 2001). Many created wetlands are constructed from sandy dredge spoil (Cammen 1976; Broome et al. 1988; Zedler & Lindig-Cisneros 2000), which can take 15–30 years to develop organic matter levels comparable to those in natural areas (Craft et al. 1988), potentially limiting macrofaunal food availability in those sites. In addition, vegetation structure can affect the amount of habitat available for foraging or shelter from predators (Moy & Levin 1991; Scatolini & Zedler 1996; Posey et al. 1997; Talley & Levin 1999). However, establishment of stands of vegetation, often the focus of restoration efforts (Broome et al. 1988), does not insure that complementary habitat types such as mudflat or tidal creeks will also be successfully created, despite their importance for macrofaunal communities (Minello et al. 1994; Zedler 1996).

Ontogenetic shifts in dispersal ability and tolerance of physical stress may cause colonization ability to differ among age classes. Many marine invertebrates have a planktonic larval stage, but juveniles of species with direct development exhibit a wide array of alternative dispersal mechanisms, including floating on water surface tension and rafting on macroalgal mats (Highsmith 1985). In addition, juveniles may be less tolerant than adults of abiotic stressors, particularly desiccation (McCloy 1979; Gosselin 1997).

Our focal organism, *Cerithidea californica* (California horn snail), is an abundant (often 1,000/m^2) (Race 1981) epibenthic gastropod in coastal wetlands from Tomales Bay, California, to central Baja California, Mexico (Macdonald 1969). Highest abundances occur in mudflats and tidal creeks, but they are also found in vegetated areas (McCloy 1979). *Cerithidea californica* is closely associated with the sediment as a grazer on the benthic microalgal community (Whitlatch & Obrebski 1980). *Cerithidea californica* has poor dispersal ability stemming from direct development and low adult vagility (Race 1981), though juveniles have frequently been noted to float on the surface tension of the water, which may increase their dispersal ability (McCloy 1979; Race 1981).

The objective of this study was to compare the spatial and temporal patterns of *C. californica* density in a newly created coastal wetland to those population attributes in an adjacent natural site. We predicted that: (1) characteristics of the created site, including high sand content, low sediment moisture and organic content, and low plant cover, would correspond to low snail densities, and (2) the colonization rate of the created site would be slow due to the limited dispersal ability of this snail.

Methods

Study Site

The study site was a 1.4-ha created wetland and a similar area of an adjacent natural site within a tidal wetland in Mugu Lagoon, Naval Base Ventura County, southern California (34°11′ N, 119°12′ W) (Fig. 1). Historically, the created site was a combination of open lagoon and salt marsh, but it was filled to upland elevation with sandy dredge spoils from the main lagoon circa 1950. Dredging the site to tidal elevation in fall 1997 created an area of mudflat and tidal creeks with graded banks around the perimeter. Planting of native salt marsh plants (*Salicornia virginica* [pickleweed], *Jaumea carnosa* [saltmarsh daisy], *Frankenia salina* [alkali heath], and *Distichlis spicata* [saltgrass]) in March 1998 on the graded bank between 0.4 and 0.6 m above mean sea level (MSL) was supplemented by natural plant recruitment. The natural site is immediately adjacent to the created area and is comprised of dense *S. virginica*-dominated stands, sinuous tidal creeks, and small mudflat areas.

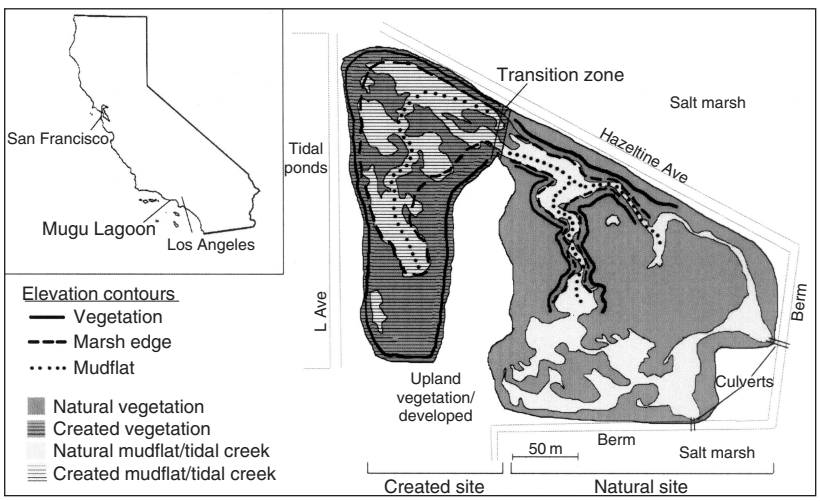

Figure 1. Schematic of study site modified from an aerial photograph.

In June 1998, we identified three elevation contours following the entire perimeter of the created site and an approximately equivalent area of the natural site (Fig. 1). The upper contour (0.58 ± 0.01 m above MSL) was placed in the salt marsh vegetation and designated as the vegetation elevation, the middle contour at the vegetation–mudflat interface (0.42 ± 0.01 m above MSL) was designated as marsh edge, and the mudflat elevation contour was approximately midway between the banks of vegetation and at varying elevation, about 0.3 m above MSL. We established 0.25-m^2 plots every 10 m along these elevation contours. We used a surveying level to insure that all plots along the vegetation and marsh edge contours lay at the same elevation. Initial plot replication was unequal (44, 44, and 8 in created site vegetation, marsh edge, and mudflat, respectively, and 11, 23, and 5 in natural site vegetation, marsh edge, and mudflat), due to the regular spacing of the plots and the unequal areas of the different habitat types. In April 2000, replication was adjusted to 10 plots in each habitat type in each site by placing plots approximately every 5 m in the mudflat elevation and in the natural site and randomly selecting 10 of the originally designated plots at the other elevations.

Population Monitoring

We monitored *C. californica* abundance and size structure in the created site and adjacent natural site in July 1998, July 1999, July 2000 (marsh edge and mudflat only; vegetation was excluded on this date due to logistical constraints), and August 2001. To quantify snail density and size frequency, we collected snails from each plot both from the surface and within the top 1 cm of sediment. *Cerithidea californica* may occasionally climb *S. virginica* stems, but we focused on snails on the sediment at all elevations, because the sediment surface is the primary substrate occupied by this species (McCloy 1979). Due to the typically high abundances of *C. californica*, we divided a 0.25-m^2 quadrat into 0.01-m^2 subquadrats, randomly selected five of these for exhaustive sampling, and extrapolated to estimate the density of the entire plot. If these five subquadrats yielded fewer than a total of 20 snails (corresponding to 400 snails/m^2), we gathered all snails within the 0.25-m^2 plot. Immediately after collection, we counted snails in each of four 10-mm size classes ($\leq$10 mm, 10.1–20 mm, 20.1–30 mm, and >30 mm). Snails less than 2 mm in length were not reliably detectable and were not included in density and size frequency counts. These size classes approximately correspond to age groups: juvenile ($\leq$10 mm), subadult (10.1–20 mm), and mature adult (>20 mm) (McCloy 1979). After measurement in the field, snails were returned to the plots from which they were collected.

We performed a one-way repeated measures ANOVA on total snail density within each elevation, where the factor was site (natural vs. created) and the repeated measure was year (1998–2001). All data were tested for normality and variances for homoscedasticity and transformed if necessary to conform to assumptions of ANOVA.

To examine snail population size structure in the natural and created sites, we converted size data to frequencies. For July 1998, July 1999, July 2000, and August 2001, we performed Kolmogorov–Smirnov tests comparing natural versus created size frequency distributions within each year and elevation. A total of 11 paired comparisons (k) were made ([4 years $\times$ three elevations] $-$ vegetation elevation in 2000), so we adjusted the significance p value via the sequential k comparison by the Dunn–Sidák method for multiple comparisons, where $\alpha' = 1-(1-\alpha)^{1/k'}$ and α' = the adjusted alpha value, α = the experiment-wise error rate (0.0500), and k' = the adjusted number of paired comparisons (k, $k-1$, $k-2$,...) following each sequential comparison (Sokal & Rohlf 1995). The first iteration of the sequential k comparison yielded an adjusted alpha of 0.0046 and the fifth iteration yielded 0.0073 (no additional iterations were necessary because the remainder of the p values were greater than 0.0500).

Distance

To evaluate *C. californica* dispersal ability, we examined whether the relationship between created site snail density and the distance from the natural site changed over time. From an aerial photograph of the site (Radman Aerial Surveys, Sacramento, CA, U.S.A.), we measured the distance of each plot in the created site from the center of the natural/created site transition zone, defined as a 20-m wide section separating the two sites (Fig. 1). We assumed that all snails dispersed into the created site from the midpoint of the transition area and that the snails traveled along the shortest route from the transition zone to the plots in which they were found without passing through the vegetation elevation. Analysis of covariance (ANCOVA) was employed within the marsh edge and mudflat elevations to statistically compare the slopes of the regressions of snail density on distance among years. Average snail densities in the vegetation elevation were typically less than 10/m^2, and this elevation therefore was excluded from this analysis. The dependent variable was snail density, the independent variable was year, and the covariate was distance from the transition zone. This analysis was performed separately for juvenile (<10 mm), subadult (10–20 mm), and adult (>20 mm) size classes.

Habitat Characteristics

To quantify physical and biological differences between sites, we measured algal, plant, and soil attributes in July 1998. We estimated percent cover of macroalgal mats (mainly *Enteromorpha* spp. [Chlorophyta]) and vascular plants within the plots by the point-intercept method

(Robson & Sheehy 1981) using a 0.25-m^2 plexiglass sheet drilled with 49 holes to accommodate a vertically oriented laser pointer.

We took four 2-cm deep, 5-cm diameter sediment cores from each plot in July 1998. Cores from each plot were homogenized and dried to determine percent moisture. Sediment organic content was determined by loss on ignition at 400°C for 10 hr. Relative salinity was recorded by filtering a portion of a saturated soil paste (Richards 1954) through two layers of no. 2 Whatman filter paper onto a Leica temperature-compensated refractometer. Grains were separated into percent sand, silt, and clay using the hydrometer fractionation method of Bouyoucos (1962).

All habitat characteristics were analyzed using two-factor designs. If assumptions of ANOVA were not met, we employed the Scheirer–Ray–Hare extension of the nonparametric Kruskal–Wallis test (Sokal & Rohlf 1995), where the factors were site and elevation. This test was performed for vascular plant and macroalgal percent cover. These data had a strongly bimodal character, because macroalgae and vascular plants tended to be either abundant or absent. Macroalgal cover was less than 5% at the vegetation elevation in both sites, and vascular plants were absent from the mudflat, and so those elevations were excluded from the respective statistical analyses. The Scheirer–Ray–Hare extension was also applied to sediment percent moisture, which had a strongly bimodal distribution. For all other habitat characteristics, data transformations resulted in agreement with the assumptions of ANOVA. A two-way ANOVA was used for each characteristic, where the factors were site and elevation.

Multiple regression was employed to evaluate the relationship of the range of natural and created site habitat characteristics to *C. californica* population characteristics. Collinearity between independent variables was tested by calculating tolerance values. Because sand, silt, and clay add up to 100%, which creates a singular correlation matrix (where there is a linear relationship between some of the variables), we excluded the intermediate grain size group (silt) from this analysis. Following the exclusion of silt, all tolerance values were greater than 0.1, indicating a low degree of collinearity (Quinn & Keough 2002). Thus, habitat characteristics were used as independent variables in multiple regressions, where the dependent variables were densities of each size class of snails and the percentage of the population in each size class.

To determine whether some of the variability in habitat characteristics in the created site was explained by distance from the natural site transition zone, we also performed a series of seven simple regressions of each habitat characteristic on distance from the transition zone. We adjusted the significance p value via the sequential k comparison by the Dunn–Sidák method for multiple comparisons (Sokal & Rohlf 1995); the first iteration yielded an adjusted alpha of 0.0073 and the second iteration yielded 0.0085 (no additional iterations were necessary).

Results

Population Structure

Snail density was always lower at the vegetation elevation than at the marsh edge and mudflat (Fig. 2). There was a significant interaction between site and year for total snail density at the vegetation elevation (repeated measures ANOVA, $F = 5.045$, $df = 2$, $p = 0.0117$). Snail density was

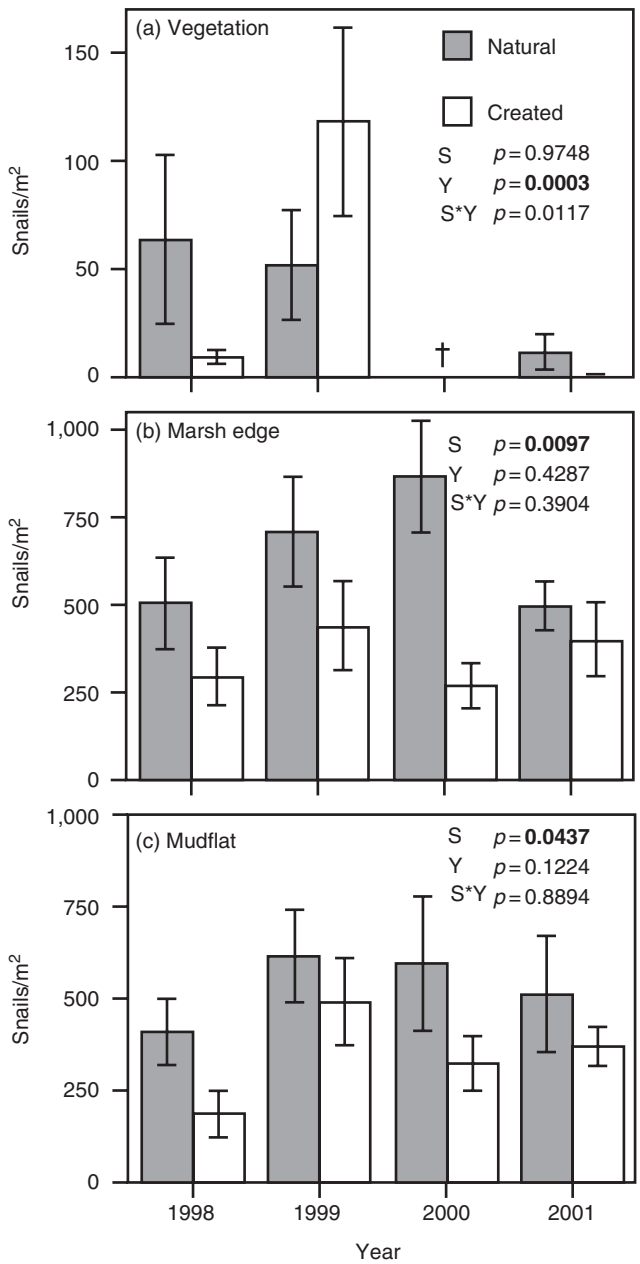

Figure 2. *Cerithidea californica* density each summer from 1998 to 2001 in a natural and a created wetland at (a) vegetation, (b) marsh edge, and (c) mudflat elevations. p values from repeated measures ANOVA are reported; significant values are in bold type. S = site, Y = year. Bars represent standard error. † indicates no data collected. Note different y-axes.

nearly an order of magnitude higher in the natural site than in the created site in 1998, but in 1999, snail density was higher in the created site (Fig. 2a). In 2001, snail density was lower than in previous years in both sites and was slightly higher in the natural than in the created site.

The highest snail densities occurred at the marsh edge elevation. There was a significant effect of site ($F = 8.370$, $df = 1$, $p = 0.0097$) but not year because snail density was higher in the natural site throughout the study period (Fig. 2b). The difference between sites was smaller in 2001 than in all other years, but the largest difference occurred in 2000, suggesting that created site densities were not approaching those in the natural site.

At the mudflat elevation, there was also a significant effect of site ($F = 5.188$, $df = 1$, $p = 0.0437$) but not year. Snail density was higher in the natural site throughout the study period, with the largest differences between sites in 1998 and 2000 and smaller differences in 1999 and 2001, suggesting that created site densities were not approaching those in the natural site (Fig. 2c).

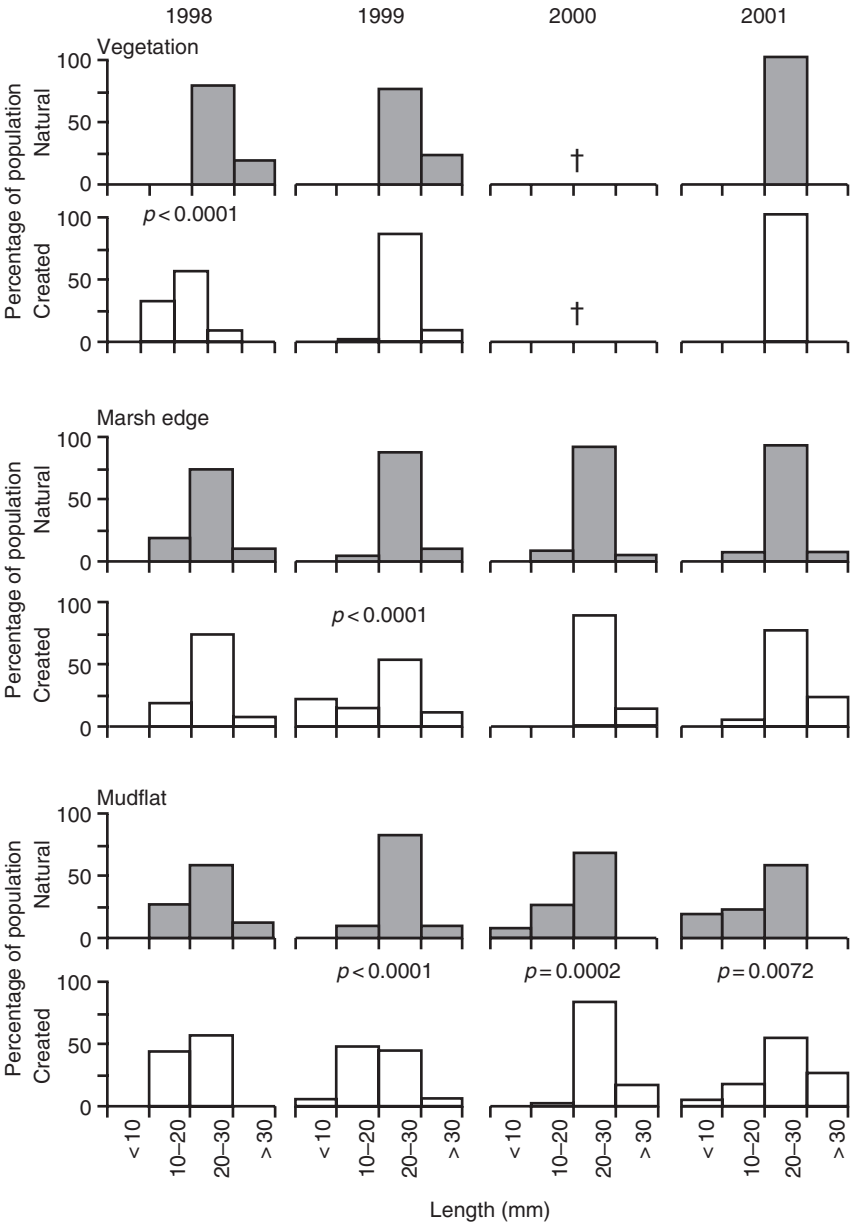

Figure 3. Comparison of natural and created site *Cerithidea californica* size frequency distributions at each elevation in the summer over 4 years. *p* values from Kolmogorov–Smirnov tests denote significant differences between natural and created site distributions. † indicates no data collected.

Snail populations in both sites were usually dominated by adult (>20 mm) snails, but pulses of juvenile (<10 mm) and subadult (10–20 mm) snails occurred at various times at all elevations (Fig. 3). At the vegetation elevation, adult snails (>20 mm) comprised nearly 100% of the population on most dates in both sites. The exception was a pulse of subadult snails (10–20 mm) in the created site in 1998, the summer after the site was opened to tidal flow. This pulse created a significant difference in the size frequency distributions between sites at this elevation (Kolmogorov–Smirnov, $p < 0.0001$) in 1998 but not in any other year (all $p > 0.1000$).

At the marsh edge elevation, the natural site population was more than 75% adult (>20 mm) snails throughout the study period (Fig. 3). The created site population was more than 75% adult snails except in 1999, when a pulse of juvenile (<10 mm) snails occurred. This pulse of smaller snails created a significant difference in the size frequency distributions between sites at the marsh edge elevation in 1999 ($p < 0.0001$) but not in any other year (all $p > 0.1000$).

At the mudflat elevation, there were more juvenile and subadult snails (up to 35–50% of the population) than at the other elevations in both sites in all years (Fig. 3). Subadult snails were common in both sites in 1998, and size frequency distributions were similar between sites ($p > 0.1000$). Distributions differed between sites in the other 3 years, but patterns varied among years. In 1999 ($p < 0.0001$), a large proportion of the created site population was comprised of subadult (10–20 mm) snails, but in 2000 ($p = 0.0002$), subadult snails were more common in the natural site. In 2001 ($p = 0.0072$), there were more juveniles (<10 mm) in the natural site and more of the largest (>30 mm) snails in the created site.

Distance

There was a significant effect of distance on adult snail density at both the marsh edge (ANCOVA, $F = 22.628$, $df = 1$, $p < 0.0001$) and mudflat ($F = 35.994$, $df = 1$, $p < 0.0001$) elevations (Fig. 4), but no significant effect of year (both $p > 0.1000$), suggesting that throughout the study period, adult snail density decreased as distance from the natural site increased. In addition, there were no significant interactions between distance and year on snail density for adult snails at either elevation (both $p > 0.1000$), suggesting that the relationship between snail density and distance from the transition zone was consistent across years. Neither juvenile nor subadult snail density was significantly related to distance from the transition zone or year (all $p > 0.0500$; patterns not shown).

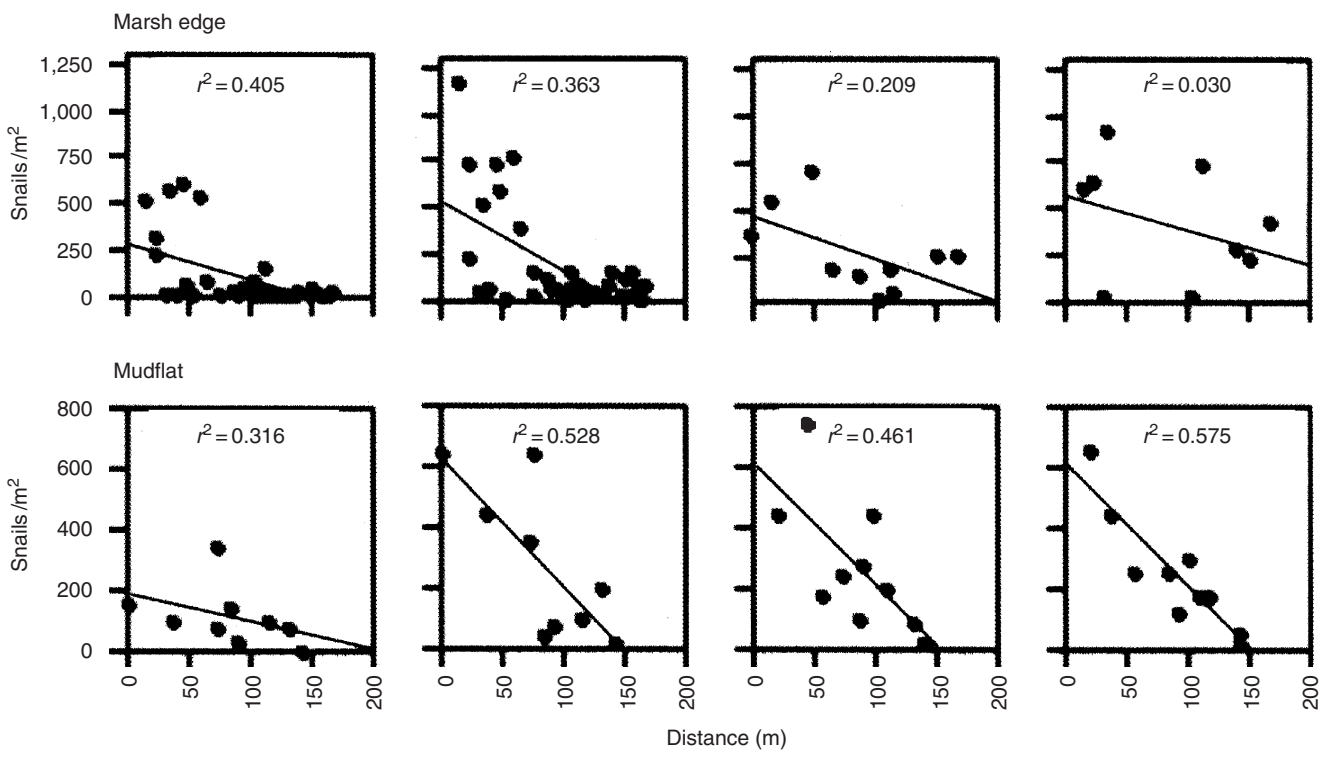

Figure 4. Relationship between the summer density of adult *Cerithidea californica* in the created site and distance from the natural site over 4 years at the marsh edge and mudflat elevations. r^2 values from simple regressions are reported. Note different *y*-axes.

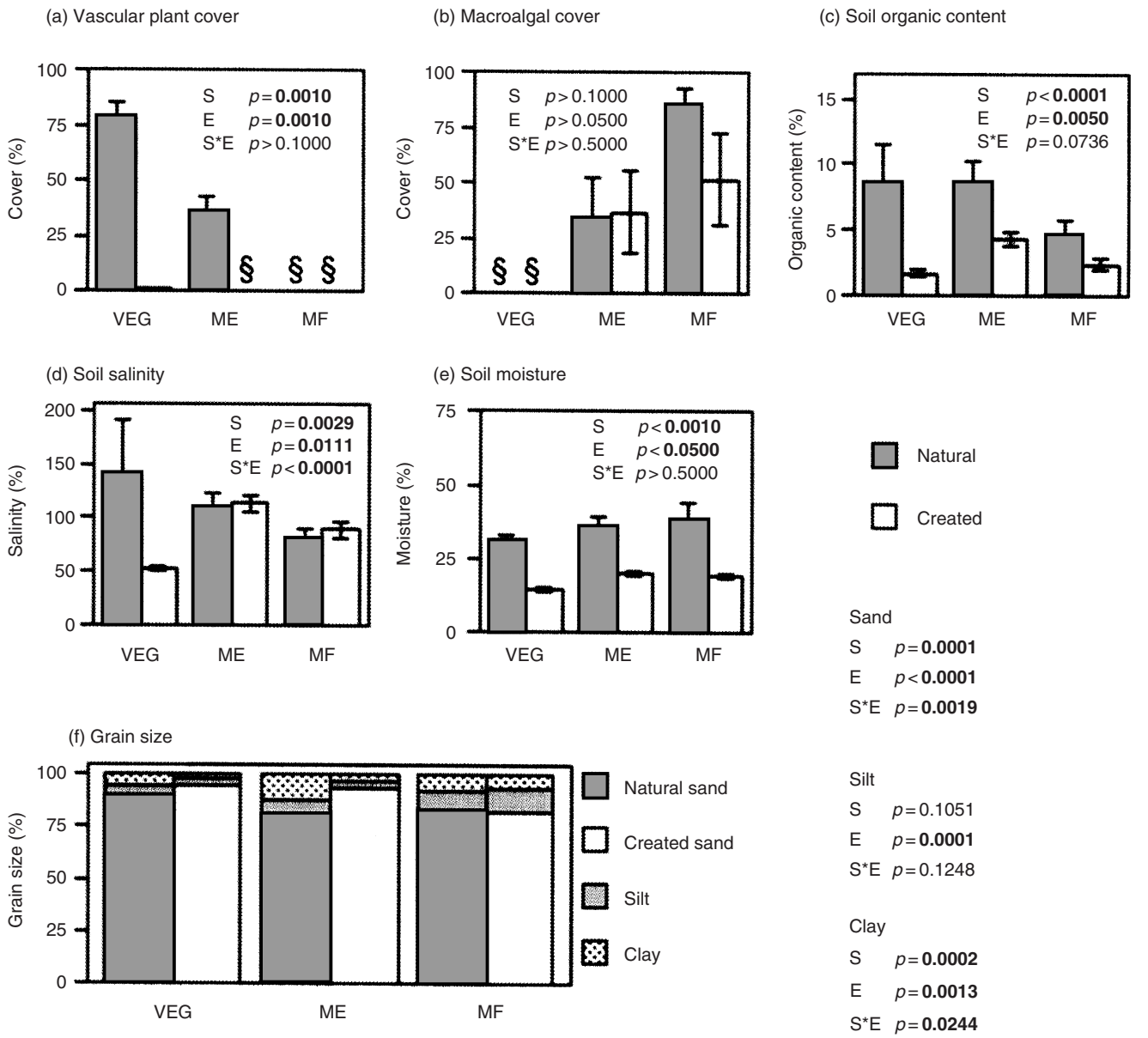

Figure 5. Habitat characteristics of natural and created sites at vegetation (VEG), marsh edge (ME), and mudflat (MF) elevations: (a) vascular plant cover, (b) macroalgal cover, (c) sediment organic content, (d) sediment salinity, (e) sediment moisture, and (f) grain size. p values from two-way Kruskal–Wallis tests or ANOVA are reported; significant values are in bold type. S = site, E = elevation. Bars represent standard error. § indicates less than 1% cover.

Habitat Characteristics

There was a significant effect of both site (Kruskal–Wallis, $H = 14.425$, $df = 1$, $p < 0.0010$) and elevation ($H = 156.691$, $df = 2$, $p < 0.0010$) on vascular plant cover, with no significant interactions between factors. Plant cover was higher in the natural site and at the vegetation elevation (Fig. 5a). Macroalgal cover did not significantly vary with site or between the marsh edge and mudflat (all $p > 0.0500$), although there tended to be more macroalgae in the natural than in the created mudflat (Fig. 5b).

Sediment organic content was significantly affected by both site (ANOVA, $F = 33.483$, $df = 1$, $p < 0.0001$) and elevation ($F = 5.782$, $df = 2$, $p = 0.0050$). Overall, organic content was higher in the natural site (Fig. 5c). Organic content tended to be lowest at the mudflat elevation and the largest differences between sites occurred at the vegetation elevation.

There was a significant interaction between site and elevation ($F = 11.235$, $df = 2$, $p < 0.0001$) for soil salinity, because the sites appeared to differ only at the vegetation elevation (Fig. 5d).

Sediment percent moisture varied significantly with site (Kruskal–Wallis, $H = 52.517$, $df = 1$, $p < 0.0010$) and with elevation ($H = 6.587$, $df = 2$, $p < 0.0500$). Moisture was

higher in the natural site overall and lowest at the vegetation elevation in both sites (Fig. 5e).

A significant interaction occurred between site and elevation for percent sand (ANOVA, $F = 6.870$, $df = 2$, $p = 0.0019$) and for percent clay ($F = 3.929$, $df = 2$, $p = 0.0244$). Sand content tended to be higher in the created site than in the natural site at the vegetation and marsh edge elevations, but the mudflat elevation had similar sand content in both sites (Fig. 5f). Clay content showed the opposite pattern: there was more clay in the natural site than in the created site, but only at the vegetation and marsh edge elevations. Clay content was similar between sites at the mudflat elevation. Silt content was significantly affected by elevation ($F = 10.550$, $df = 2$, $p = 0.0001$) but not site ($p > 0.1000$), tending to be higher in the mudflat elevation than in the vegetation or marsh edge elevations in both sites.

Multiple regressions of snail density and the percentage of the snail population in each size class on habitat characteristics suggested that sediment moisture ($p < 0.0001$) and organic content ($p = 0.0476$) were positively related to adult snail density (cumulative $r^2 = 0.551$). The percentage of adults in the population was also positively related to sediment moisture ($p = 0.0200$, $r^2 = 0.230$). Sediment moisture ($p < 0.0001$) and organic content ($p = 0.0037$) were positively related to subadult snail density, though these habitat characteristics explained less variability than for adults ($r^2 = 0.471$). The percent of subadults in the population was negatively related to sediment moisture ($p = 0.0256$), vascular plant cover ($p = 0.0429$), and to a lesser degree, sediment organic content ($p = 0.0526$, cumulative $r^2 = 0.334$). Habitat characteristics did not explain any variability in juvenile snail density or relative abundance (all $p > 0.1000$).

Simple regressions indicated that small but significant portions of the variability in algal cover ($p = 0.0021$, $r^2 = 0.162$) and vascular plant cover ($p = 0.0044$, $r^2 = 0.141$) were explained by distance from the natural site. Neither of those factors explained any variability in snail density, suggesting that habitat characteristics and distance probably acted independently on snail density.

Discussion

Cerithidea californica densities remained lower and, at the mudflat elevation, size frequency distributions differed from those in the natural site after 4 years. Although we surveyed only one created area and one relatively natural site, variable densities among years cast doubt on whether the created site snail population was on a recovery trajectory toward the natural system. Differences in gastropod densities commonly persist between natural and created areas in tidal wetlands. In San Diego, California, Scatolini and Zedler (1996) sampled epibenthic invertebrate populations in a *Spartina foliosa* (cordgrass)-dominated wetland, and likewise found created site densities of *C. californica* in a 4-year-old created site to be only one-third of those in a natural area. Wetland gastropods in other regions have shown similar patterns of lower densities in created areas for several years following site restoration. In North Carolina, *Nassarius obsoletus* (eastern mud snail) achieved only 50% of natural densities in a 27-month-old restoration site (Levin et al. 1996). In England, *Hydrobia ulvae* (mud snail) rapidly colonized a mudflat following restoration of tidal flooding, but after 4 years, snail densities remained one-third of those in natural areas (Evans et al. 1998). Reduced snail densities in our study site and other created wetlands were likely caused by some combination of limited dispersal ability and unsuitable habitat characteristics.

Dispersal ability is a fundamental factor influencing colonization of created habitats (Mortimer et al. 2002). Often those organisms with limited mobility, such as those that lack a planktonic larval stage or have low adult vagility, colonize created habitats slowly over many years, if they colonize at all (Johannesson & Johannesson 1995; Brown et al. 1997; Lehtinen & Galatowitsch 2001; Mortimer et al. 2002). Such species often utilize an alternative mechanism for dispersing into new habitat, such as rafting on macroalgal mats or floating on the water surface (Highsmith 1985), although it is usually less effective than planktonic larval dispersal (Johannesson & Johannesson 1995). *Cerithidea californica* has both direct development and low adult vagility (Race 1981). Accordingly, despite the proximity of the created site to the natural source population in this study, dispersal ability probably partially limited snail density in the created site. However, if dispersal ability had been the sole factor influencing snail colonization, we would have expected the strength of the relationship between snail density and distance from the transition zone to decrease over time. The continued importance of distance for adult snail densities indicated that additional factors, namely habitat characteristics, probably also limited snail colonization of the created site.

A variety of habitat suitability factors may contribute to snail and other invertebrate scarcity in created wetlands. Lower food availability in created than in natural sites often correlates to reduced macrofaunal abundances (Levin & Talley 2000). In the Gulf of Mexico, some caridean shrimp species were 33% smaller in created areas, possibly because of low organic matter concentration (Minello & Webb 1997). Likewise, the created site at Mugu Lagoon had lower sediment organic content than in the natural site, a common occurrence in sandy sediments in created wetlands (Craft et al. 1988; Levin & Talley 2000; Zedler & Lindig-Cisneros 2000; Campbell et al. 2002). In addition, higher vascular plant cover in the natural site may have increased sediment organic content through the input of detrital material. However, in our study, lower sediment organic content in the created site corresponded to an overall decrease in snail abundance rather than a shift toward smaller snail sizes. Benthic chlorophyll *a* concentration, which reflects the total biomass of the benthic

microalgal food source for *C. californica*, was actually higher in the created site (Armitage 2003), due in part to the lower vascular plant cover and higher light availability (Levin & Talley 2000), but the quality of the microalgal food source may differ between sites. Diatoms are generally considered to be the snails' primary food source (Whitlatch & Obrebski 1980), but the larger sediment grains in the created site supported fewer diatoms and more cyanobacteria than did the finer-grained sediment of the natural site, and cyanobacteria may be toxic or have low nutritive value for the snails (Armitage 2003).

Vascular plant structure can influence not only benthic food availability but also the impact of predators. With its low vegetation cover, the created site attracted more migrating shorebirds than did the natural site (Armitage 2003). Shorebirds, particularly *Catoptrophorus semipalmatus* (willet), are potential predators of juvenile and subadult *C. californica* (McCloy 1979; Sousa 1993) and may reduce snail abundance where they forage. Intense predation pressure from dense *C. semipalmatus* aggregations in the created site probably exerted a strong but temporally variable influence on juvenile and subadult snails that may have been more important than habitat characteristics in limiting the ability of small *C. californica* to establish in the created site.

Although we quantified habitat features only in the first year of the study, long-term studies often indicate that the development of natural physical and biotic characteristics in created wetland sites may take many years. Created site sediments are often sandier and less organic than sediment in natural areas (Lindau & Hossner 1981; Zedler & Lindig-Cisneros 2000; Campbell et al. 2002). In fact, some projections of created site development predict that more than 30 years may be required for sediment macroorganic matter and nutrient pools to reach natural levels (Craft et al. 1988). Marsh vegetation tends to approach natural cover levels more quickly, sometimes within 4 years (LaSalle et al. 1991), although plant species diversity and canopy structure and complexity may continue to differ from natural conditions for many additional years (Zedler 1993; Campbell et al. 2002). Thus, it is probable that the measured physical and biotic characteristics continued to influence the relative *C. californica* scarcity in our created site throughout the study period.

The degree to which limited dispersal ability and habitat characteristics influenced *C. californica* density in the created site varied among size classes. Adult snail density and relative abundance were affected by some physical habitat characteristics, and the relationship between adult density and distance from the natural site suggests that dispersal ability may have been important as well. The primary means of adult *C. californica* movement is crawling along the sediment surface (Race 1981). This slow locomotion may delay colonization of new habitats, but may also provide adult snails with more time to react to their physical habitat, explaining the stronger relationship between snail density and habitat characteristics in adults than in smaller-size classes. Juvenile density and relative abundance in the population did not exhibit a close relationship with either habitat characteristics or distance, possibly because juvenile dispersion may have arisen from largely stochastic dispersal events such as floating on the surface tension of the water (McCloy 1979; Race 1981) or rafting on ephemeral but locally abundant mats of macroalgae (Highsmith 1985; Kamer et al. 2001). Like juvenile snails, the highly variable density of subadult snails in the created site and the lack of a correlation with distance from the natural site may reflect temporally stochastic dispersal events arising from their rafting abilities (McCloy 1979). In addition, the level of influence of habitat characteristics on subadult density and relative abundance was intermediate between the relatively strong adult relationship and nonexistent juvenile relationship, suggesting that habitat suitability may increasingly affect colonization patterns as snails mature. The correlation of the relative abundances of adult and subadult but not juvenile snails to habitat characteristics, particularly sediment moisture, indicates that habitat characteristics had stronger influences on larger snails and that smaller snail densities were probably driven by stochastic dispersal and colonization events.

This study supported our predictions that both habitat characteristics and dispersal ability would limit snail colonization of the created site, though we observed substantial differences in the roles of these factors among size classes of snails. The strong relationships between adult snail density and habitat characteristics such as sediment moisture and organic content suggest that attention to such detailed habitat features may facilitate successful restoration of epibenthic invertebrate communities. In addition, even for this small created site in close proximity to a natural area, dispersal ability may have also limited created site colonization. Larger snails with limited mobility predictably but slowly colonized the created site, whereas smaller snails colonized in large numbers but at unpredictable spatial and temporal intervals. This study demonstrated that monitoring programs, in addition to manipulative experiments, can contribute to the planning of successful habitat restoration efforts by identifying the limitations of organisms such as *C. californica* in colonizing created sites.

Acknowledgments

We thank T. Keeney and the U.S. Navy for providing access to the research site. Many thanks to R. R. Vance and R. F. Ambrose for thoughtful insight into the study design and analysis and two anonymous reviewers for comments that improved the manuscript. We deeply appreciate the endurance of the many field crews who assisted with snail measurement. This project was funded in part by predoctoral awards from the UCLA Institute of the Environment and the Association for Women in Science and a UC Coastal Environmental Quality Initiative Graduate Fellowship to A.R.A. and a grant from the EPA (R827637) to P.F.

LITERATURE CITED

Armitage, A. R. 2003. Community structure and trophic interactions in restored and natural estuarine mudflats: complex trophic cascades and positive and negative effects of nutrients. Ph.D. thesis. University of California, Los Angeles.

Block, W. M., A. B. Franklin, J. P. Ward, J. L. Ganey, and G. C. White. 2001. Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. Restoration Ecology **9:**293–303.

Bouyoucos, G. J. 1962. Hydrometer method improved for making particle size analyses of soils. Agronomy Journal **54:**464–465.

Broome, S. W., E. D. Seneca, and W. W. Woodhouse, Jr. 1988. Tidal salt marsh restoration. Aquatic Botany **32:**1–22.

Brown, S. C., K. Smith, and D. Batzer. 1997. Macroinvertebrate responses to wetland restoration in northern New York. Environmental Entomology **26:**1016–1024.

Cammen, L. M. 1976. Macroinvertebrate colonization of *Spartina* marshes artificially established on dredge spoil. Estuarine and Coastal Marine Science **4:**357–372.

Campbell, D. A., C. A. Cole, and R. P. Brooks. 2002. A comparison of created and natural wetlands in Pennsylvania, USA. Wetlands Ecology and Management **10:**41–49.

Craft, C. B., S. W. Broome, and E. D. Seneca. 1988. Nitrogen, phosphorus and organic carbon pools in natural and transplanted marsh soils. Estuaries **11:**272–280.

Evans, P. R., R. M. Ward, M. Bone, and M. Leakey. 1998. Creation of temperate-climate intertidal mudflats: factors affecting colonization and use by benthic invertebrates and their bird predators. Marine Pollution Bulletin **37:**535–545.

Gosselin, L. A. 1997. An ecological transition during juvenile life in a marine snail. Marine Ecology Progress Series **157:**185–194.

Highsmith, R. C. 1985. Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. Marine Ecology Progress Series **25:**169–180.

Johannesson, K., and B. Johannesson. 1995. Dispersal and population expansion in a direct developing marine snail (*Littorina saxatilis*) following a severe population bottleneck. Hydrobiologia **309:**173–180.

Kamer, K., K. A. Boyle, and P. Fong. 2001. Macroalgal bloom dynamics in a highly eutrophic southern California estuary. Estuaries **24:**623–635.

Kneib, R. T. 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. Estuaries **7:**392–412.

LaSalle, M. W., M. C. Landin, and J. G. Sims. 1991. Evaluation of the flora and fauna of a *Spartina alterniflora* marsh established on dredged material in Winyah Bay, South Carolina. Wetlands **11:**191–208.

Lehtinen, R. M., and S. M. Galatowitsch. 2001. Colonization of restored wetlands by amphibians in Minnesota. American Midland Naturalist **145:**388–396.

Levin, L. A., and T. S. Talley. 2000. Influences of vegetation and abiotic environmental factors on salt marsh invertebrates. Pages 661–708 in M. P. Weinstein and D. A. Kreeger, editors. Concepts and controversies in tidal marsh ecology. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Levin, L. A., D. Talley, and G. Thayer. 1996. Succession of macrobenthos in a created salt marsh. Marine Ecology Progress Series **141:**67–82.

Lindau, C. W., and L. R. Hossner. 1981. Substrate characterization of an experimental marsh and three natural marshes. Soil Science Society of America Journal **45:**1171–1176.

Macdonald, K. B. 1969. Molluscan faunas of Pacific coast salt marshes and tidal creeks. Veliger **11:**399–405.

McCloy, M. J. 1979. Population regulation in the deposit feeding mesogastropod *Cerithidea californica* as it occurs in a San Diego salt marsh habitat. M.Sc. thesis. San Diego State University, San Diego, California.

Minello, T. J., and J. W. Webb, Jr. 1997. Use of natural and created *Spartina alterniflora* salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA. Marine Ecology Progress Series **151:**165–179.

Minello, T. J., R. J. Zimmerman, and R. Medina. 1994. The importance of edge for natant macrofauna in a created salt marsh. Wetlands **14:**184–198.

Mortimer, S. R., R. G. Booth, S. J. Harris, and V. K. Brown. 2002. Effects of initial site management on the Coleoptera assemblages colonising newly established chalk grassland on ex-arable land. Biological Conservation **104:**301–313.

Moy, L. D., and L. A. Levin. 1991. Are *Spartina* marshes a replaceable resource? A functional approach to evaluation of marsh creation efforts. Estuaries **14:**1–16.

Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997. Ecological theory and community restoration ecology. Restoration Ecology **5:**291–300.

Parsons, L. S., and J. B. Zedler. 1997. Factors affecting reestablishment of an endangered annual plant at a California salt marsh. Ecological Applications **7:**253–267.

Passell, H. D. 2000. Recovery of bird species in minimally restored Indonesian tin strip mines. Restoration Ecology **8:**112–118.

Posey, M. H., T. D. Alphin, and C. M. Powell. 1997. Plant and infaunal communities associated with a created marsh. Estuaries **20:**42–47.

Powell, A. N., and C. L. Collier. 2000. Habitat use and reproductive success of western snowy plovers at new nesting areas created for California least terns. Journal of Wildlife Management **64:**24–33.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, United Kingdom.

Race, M. S. 1981. Field ecology and natural history of *Cerithidea californica* (Gastropoda: Prosobranchia) in San Francisco Bay. Veliger **24:**18–27.

Richards, L. A. 1954. Diagnosis and improvement of saline and alkali soils. Agriculture Handbook No. 60. U.S. Department of Agriculture, Washington, D.C.

Robson, M. J., and J. E. Sheehy. 1981. Leaf area and light interception. Pages 115–140 in J. Hodgson, R. D. Baker, A. Davies, A. S. Laidlaw, and L. D. Leaver, editors. Sward measurement handbook. British Grassland Society, London, United Kingdom.

Sacco, J. N., E. D. Seneca, and T. R. Wentworth. 1994. Infaunal community and development of artificially established salt marshes in North Carolina. Estuaries **17:**489–500.

Scatolini, S. R., and J. B. Zedler. 1996. Epibenthic invertebrates of natural and constructed marshes of San Diego Bay. Wetlands **16:**24–37.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edition. W.H. Freeman, New York.

Sousa, W. P. 1993. Size-dependent predation on the salt-marsh snail *Cerithidea californica* Haldeman. Journal of Experimental Marine Biology and Ecology **166:**19–37.

Talley, T. S., and L. A. Levin. 1999. Macrofaunal succession and community structure in *Salicornia* marshes of southern California. Estuarine, Coastal and Shelf Science **49:**713–731.

Whitlatch, R. B., and S. Obrebski. 1980. Feeding selectivity and coexistence in two deposit feeding gastropods. Marine Biology **58:**219–226.

Williams, G. D., and J. B. Zedler. 1999. Fish assemblage composition in constructed and natural tidal marshes of San Diego Bay: relative influence of channel morphology and restoration history. Estuaries **22:**702–716.

Zajac, R. N., and R. B. Whitlatch. 2001. Response of macrobenthic communities to restoration efforts in a New England estuary. Estuaries **24:**167–183.

Zedler, J. B. 1993. Canopy architecture of natural and planted cordgrass marshes: selecting habitat evaluation criteria. Ecological Applications **3:**123–138.

Zedler, J. B. 1996. Coastal mitigation in southern California: the need for a regional restoration strategy. Ecological Applications **6:**84–93.

Zedler, J. B., and R. Lindig-Cisneros. 2000. Functional equivalency of restored and natural salt marshes. Pages 569–582 in M. P. Weinstein and D. A. Kreeger, editors. Concepts and controversies in tidal marsh ecology. Kluwer Academic Publishers, Dordrecht, The Netherlands.