

Benthic food-web succession in a developing salt marsh

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ABSTRACT: Ecological succession has long been a focal point for research, and knowledge of underlying mechanisms is required if scientists and managers are to successfully promote recovery of ecosystem function following disturbance. We addressed the influence of bottom-up processes on successional assemblage shifts in salt marshes, ecosystems with strong physical gradients, and how these shifts were reflected in the trophic characteristics of benthic fauna. We tracked the temporal development of infaunal community structure and food-web interactions in a young, created salt marsh and an adjacent natural marsh in Mission Bay, California, USA (1996–2003). Macrofaunal community succession in created *Spartina foliosa* habitats occurred rapidly, with infaunal densities reaching 70% of those in the natural marsh after 1 yr. Community composition shifted from initial dominance of insect larvae (surface-feeding microalgivores) to increased dominance of oligochaetes (subsurface-feeding detritivores) within the first 7 yr. Isotopic labeling of microalgae, N₂-fixing cyanobacteria, *S. foliosa* and bacteria revealed direct links (or absence thereof) between these basal food sources and specific consumer groups. In combination with the compositional changes in the macroinvertebrate fauna, the trophic patterns indicated an increase in food-web complexity over time, reflecting resource-driven marsh succession. Natural abundance stable isotope ratios of salt marsh consumers (infaunal and epifaunal macroinvertebrates, and fish) initially reflected distinctions in trophic structure between the created and natural marsh, but these diminished during successional development. Our findings suggest that changing resource availability is one of the important drivers of succession in benthic communities of restored wetlands in Southern California.

KEY WORDS: Infauna · Recovery · Resource availability · *Spartina* · Tidal marsh · Trophic relationships

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INTRODUCTION

Succession, i.e. directional changes in community attributes following perturbation, generally involves increasing diversity, biomass and trophic complexity (number of trophic groups, maximum food-chain

length, link density), while niche width decreases as taxa become more specialized (Odum 1969, Neutel et al. 2007). The successional outcome depends on multiple interactions between early and later-stage colonists, as well as abiotic conditions and historical effects (Connell & Slatyer 1977, Zajac et al. 1998,

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Fukami et al. 2005, Young et al. 2005). Although they focus on whole-community properties, theories of community assembly (Young et al. 2001) and state transition (Suding et al. 2004) do not generally consider processes involving specific interactions among species and their resources (but see Chase 2003, Neutel et al. 2007) or their predators (Olito & Fukami 2009). Here we examine successional changes in the consumer community ascribed to bottom-up processes, i.e. faunal assemblages influenced by food source availability and associated abiotic and biotic conditions (Pearson & Rosenberg 1987, Levin et al. 2006). Elucidating consumer–resource interactions along a successional gradient increases our ability to predict and enhance the development of community structure and ecological functioning after perturbations.

To study benthic succession, we used the process of restoration as it provides an example of perturbation followed by community change. The succession-based approach to restoration relies on an independent development of the consumer community and the trophic interactions therein, following reestablishment of abiotic properties, habitat structure and primary producers (Palmer et al. 1997, Suding et al. 2004). In tidal wetlands, succession is often initiated through management of tidal forcing factors, sediment properties and planting of marsh plants (Zedler 2000), with the thought that fauna will colonize and establish on their own, i.e. 'build it, and they will come'. Salt-marsh plants modify both abiotic (light levels, soil physical and chemical properties) and biotic (microalgal assemblages, above- and belowground biomass and detritus) components of the marsh. Increasing plant cover (altered structural complexity and carbon dynamics) along marsh maturity gradients shapes both structure and trophic dynamics of invertebrate assemblages (Talley & Levin 1999, Levin et al. 2006, Whitcraft & Levin 2007, Grosholz et al. 2009, Schrama et al. 2012).

Food-web structure (diversity and trophic pathways) is directly related to functions such as carbon flow and food-web stability (McCann et al. 1998). As in many other systems (Moore & Hunt 1988), food webs in salt marshes have consumers relying on both detritus and live primary producers. Vascular plant detritus was recognized early on as a highly available resource (Teal 1962), but microalgae and cyanobacteria have higher nutritional value and digestibility than detritus (Kreeger & Newell 2000), and support a number of marsh fauna (Kwak & Zedler 1997, Currin et al. 2011). Compared with young, developing salt marshes, a wider range of food sources fuels the trophic network in natural marsh habitats (Sullivan & Currin 2000, Moseman et al. 2004).

Primary restoration goals often include the recovery of both biodiversity and dynamic processes in altered ecosystems or destroyed habitats (Palmer et al. 1997). However, because of limited resources, the majority of evaluations of restoration success focus on recovery of habitat structure instead of the direct measures of community functioning needed to more accurately understand trajectories of successional development (Zedler & Lindig-Cisneros 2000). We tracked benthic community succession in salt marshes to address questions about the functional development of the food web. We tested the concept that resources contribute to the reestablishment of faunal communities through marsh restoration, hypothesizing that changes in primary producer availability would influence infaunal succession and that this would be seen in the trophic characteristics of macrofaunal consumers. By assessing temporal changes in macrofaunal community structure, we examined the hypotheses that density, diversity and composition in the created marsh would increase in resemblance to the natural salt marsh community as the vegetation structural complexity and carbon dynamics change with succession. To test whether successional changes in community composition altered trophic structure of the salt marsh ecosystem, we identified trophic linkages between 4 major food sources and primary consumers in the natural and created marsh using isotope enrichment experiments.

Additionally, we asked whether succession generates changes in properties of the isotopic niches of the consumers. We hypothesized that changes in natural abundance stable isotope signatures reflecting trophic niches would occur as food webs developed, primarily with respect to similarity, i.e. marshes would become located more closely to each other in δ -isotope space with a subsequent increase in taxon niche overlap. Higher similarity would indicate a more comparable utilization of available food sources. The created marsh was further hypothesized to show greater variability (differing isotopic path trajectory attributes, such as length, direction and/or shape) than the natural marsh. Finally, we tested whether trophic diversity and the potential for trophic redundancy varied between marshes or over time as reflected by the size of the area in isotope space occupied by benthic macrofauna. We hypothesized that the highest diversity (largest area) would occur in the intermediate stage of marsh development, with the opposite pattern for redundancy (species packing).

This study extends the data sets in Levin & Talley (2002) for infaunal structure and Currin et al. (2011) for trophic function, introduces isotope enrichment

studies to establish direct trophic links, and evaluates the data in a successional context. Our study was designed to provide insight into patterns of food-web development during community recovery (trophic succession), and also to assess stable isotopes as an approach for evaluating structural and functional dimensions of community development.

MATERIALS AND METHODS

Study sites

Directly adjacent to 12.8 ha of natural wetland (the Northern Wildlife Preserve) in Mission Bay (32° 46.8' N, 117° 14.1' W), San Diego, California, USA, lies a 2.8-ha created salt marsh (the Stribley Marsh, formerly the Crown Point Mitigation Site) (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m500p043_supp.pdf). The site was excavated to intertidal elevation (90–150 cm above mean lower low water [MLLW], mixed semi-diurnal tide) and opened to tidal flushing in December 1995. We studied trophic succession in areas that in March 1996 were planted with *Spartina foliosa* (21 individuals per 10 m²) in comparison to the community in the *Spartina* zone in the natural marsh (stem density ~700 per 10 m²). We chose matching plots in the natural marsh, showing corresponding intertidal elevation (roughly 117–122 cm above MLLW; Levin & Talley 2002), hydrology (close to the created marsh) and a plant community similar in composition to that which was expected to recruit at the created site. Comparing community development in a created habitat with that of a directly adjacent natural area excludes confounding variables, such as site-specificity and spatial differences in abiotic forcing factors. While we acknowledge that replication of created and natural marshes would be ideal, there is much to be gained from intensive study (longer-term, high level of detail) within adjacent ecosystems. Below, we address the generality of our model communities in relation to other marsh succession studies.

Benthic community structure and composition

Benthic community development was estimated using methods described in Levin & Talley (2002). Community structure and composition were assessed in planted *Spartina foliosa* in the young, created marsh, and compared with the natural area com-

posed of established *S. foliosa*. Marsh vegetation (% total plant cover, % *S. foliosa*) was quantified in 4 plots (each 2 × 5 m) per marsh using 0.25 m² quadrats (n = 5, averaged within plots). Within quadrats (1 per plot), sediment cores were taken for estimates of organic matter (%), and chlorophyll *a* (chl *a*; mg m⁻²) as a proxy for microalgal biomass. Additionally, sediment-dwelling macrofauna were sampled by coring (18.02 cm² × 6 cm, n = 1–3 quadrats per plot with core taken, averaged within plots) approximately twice a year (in spring and fall), more specifically 11 times between April 1996 and April 2003. Sampling spanned roughly the first 7 yr of the developing marsh, with a gap in sampling during 2000. Sediment samples were preserved in 8% buffered formalin with Rose Bengal. Animals (>300 µm) were sorted, identified to lowest possible taxonomic level and counted. During sorting for macrofauna, plant matter was separated from the cores for estimates of belowground biomass (g core⁻¹).

Natural abundance stable isotope ratios to depict trophic succession

Natural abundance stable isotopes allowed us to infer trophic structure within the community, as consumers' carbon ratios (¹³C:¹²C, expressed as δ¹³C) indicate resource use, and nitrogen ratios (¹⁵N:¹⁴N, δ¹⁵N) reflect trophic position (Minagawa & Wada 1984, Peterson & Fry 1987). Stable isotopes constitute a time-integrated, metabolic manifestation of realized trophic interactions, and we used this information as a proxy for flow of energy and nutrients through the food web. Here we examine the patterns of 'isotopic niches', the area in δ¹³C and δ¹⁵N space occupied by a species (Newsome et al. 2007, Layman et al. 2012). Each consumer taxon is here represented in isotope space as its mean δ¹³C and δ¹⁵N (average n = 3 samples/taxon) for a particular sampling event in a specific marsh (n = 6–18 taxa). The isotopic niche is not synonymous to, but represents part of, the trophic niche, and this allowed us to track changes occurring in trophic interactions during community development.

Collection of salt-marsh organisms for analysis of natural abundance stable isotope ratios took place in conjunction with quantitative sampling for estimation of benthic community structure, using the same plots. We collected marsh organisms during spring and fall sampling in the created and natural marsh, a total of 9 times between October 1996 and April 2003, with no sampling 1999–2000. Thereby, the first

sampling occurred 10 mo after marsh establishment and the last sampling occurred when the created marsh was more than 7 yr old. We sampled taxa belonging to primary producers (vascular plants, macroalgae, microalgae), primary consumers (infaunal and epifaunal invertebrates) and secondary consumers (fishes) in the salt marsh. Sample collection, treatment and analysis are described in Currin et al. (2011) and in the section 'Isotope sample collection and processing' of the Supplement.

Stable isotope enrichment experiment to identify food sources

Two *in situ* tracer experiments were conducted to examine trophic pathways in the *Spartina foliosa* zone of the created and adjacent natural marsh. In November 2001, we conducted a ^{13}C tracer study to assess primary grazers on salt-marsh benthic microalgae. Bulk microalgae were labeled by spraying $\text{NaH}^{13}\text{CO}_3$ solution (99 atom% ^{13}C , 1 g m^{-2}) on natural and created marsh sediments in 0.25 m^2 plots during low tide. Invertebrates were sampled immediately after tracer addition (t_0) and 24, 72 and 144 h later, and again 57 d after labeling. We collected macrofaunal ($>300\text{ }\mu\text{m}$) samples by coring, and then processed and analyzed them for stable isotopes.

The experiment was repeated in May 2002, and expanded into a multi-labeling approach that allowed us to trace trophic transfer from 4 food sources—bulk microalgae, N_2 -fixing cyanobacteria, other bacteria and detrital *Spartina foliosa*—to members of the infaunal and epifaunal communities. Phytoplankton (marsh suspended organic material, mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N} = -17.3$ and 5.4 ‰ , respectively) was not included as a possible food source, although it is important for a few marsh taxa, such as filter-feeding bivalves and pelagic fishes (Deegan & Garritt 1997, Howe & Simenstad 2007), which were generally absent from or outside the focal consumer group in this labeling experiment. The experiments were conducted in four 0.25 m^2 plots in both the natural and created marsh. We repeated the microalgae labeling procedure as in November 2001, but expanded the treatment to include both ^{13}C -labeled microalgae and ^{15}N -labeled cyanobacteria (enriched by exposure to $^{15}\text{N}_2$ -gas, 99 atom%), separating microalgal feeders that consume N_2 -fixing cyanobacteria from those that consume other microalgae such as diatoms. A second paired treatment applied to separate plots consisted of ^{13}C -labeled bacteria and ^{15}N -labeled *S. foliosa* detritus. Bacteria were labeled

by injecting ^{13}C -acetate (72 mg l^{-1}) into the upper 2 cm of the sediment. *Spartina foliosa* was labeled using a $(^{15}\text{NH}_4)_2\text{SO}_3$ solution (98 atom% $^{15}\text{NH}_4$) prior to the start of the experiment, and deployed as harvested detritus (fragmented 3.95 g plot^{-1}). Infaunal and epifaunal invertebrates were sampled from both sets of dual-labeling plots at 0, 24, 72 and 144 h after labeling, and at Day 72. See Table S1 in the Supplement for labeling values achieved for basal food sources and sampling and analysis details.

We defined incorporation ($\Delta\delta^{13}\text{C}$ or $\Delta\delta^{15}\text{N}$, ‰) as the difference between enriched and background values determined at time zero (t_0) or the natural abundance stable isotope ratios from the closest sampling date. Macrofaunal t_0 -values fell within typical ranges: $\delta^{13}\text{C}$ from -23.1 to -9.8 ‰ , and $\delta^{15}\text{N}$ from 3.7 to 11.7 ‰ (Kwak & Zedler 1997, Moseman et al. 2004). Label incorporation was categorized as none/negligible ($\Delta\delta < 10\text{ ‰}$), moderate ($10\text{ ‰} \leq \Delta\delta < 25\text{ ‰}$) or high ($\Delta\delta \geq 25\text{ ‰}$). Late uptake (where tracer incorporation was not observed until Day 72) was considered indirect, e.g. resulting from predation or leaching, with subsequent incorporation into microbial components and thus made available for consumption.

Statistical analyses

Macrofaunal community data were analyzed with univariate and multivariate methods to determine structural and compositional changes over time. We determined the effects of marsh type (natural or created marsh, $n = 4$ plots, between-subject effect) and time (spring 1996 – spring 2003, within-subject effects) on density and diversity (number of taxa, Shannon's diversity index H' [\log_e], and evenness J'), using repeated-measures ANOVA after checking that data met assumptions. Differences in infaunal community composition between the 2 marshes were determined using a repeated-measures permutational multivariate ANOVA on square-root transformed data, again with marsh type and time as factors (Bray-Curtis similarity, 9999 permutations). Multivariate dispersion did not differ within or between marshes (all $p > 0.05$), i.e. multivariate variance was homogenous between groups. Analyses were run using R (R Development Core Team 2011).

To evaluate taxonomic shifts in a trophic context, we tested for changes in isotopic niche attributes for consumers between and within marshes along succession. Differences in assemblage position in stable isotope space (centroid location), trophic diversity

(distance to centroid and standard ellipse area [SEA]) and trophic redundancy (nearest neighbor distance) were tested using nested linear models and a residual permutation procedure (Euclidean distance, 9999 permutations) (Turner et al. 2010) in R. We assessed assemblage overlap using SEAs calculated using the SIBER metrics in the SIAR package in R (Parnell et al. 2010). SEAs were corrected for underestimation when sample sizes were small ($n < 10$). Size differences of consecutive niches within marshes or between marsh types were analyzed via Bayesian inference (104 posterior draws) (Jackson et al. 2011). We evaluated differences in overall trajectories (path length, angle and shape) of created and natural consumer assemblage stable isotopes (Turner et al. 2010). We also looked at directionality of change (Rayleigh's test) in isotope ratios from early (1996–1998) to later (2001–2003) years for a subset of 12 taxa representing microalgivores, detritivores, omnivores, predators and primary producers, in the created and natural marsh (Schmidt et al. 2007).

RESULTS

Benthic community structure and composition

We studied the successional development of primary producers and the infaunal assemblage in a created salt marsh and adjacent natural marsh habitat from spring 1996 to spring 2003. In the developing marsh, the biomass of microalgae (chl *a*) rapidly increased to match natural marsh levels (within the first year; Currin et al. 2011), whereas vascular plant cover was low (0–26%) during the first 3 yr of the created marsh (Fig. 1a–c). The natural marsh showed vascular plant cover between 65 and 82%, and also higher amounts of sediment organic matter and belowground biomass (Fig. 1d) during the same time period.

The infaunal community in the created marsh changed rapidly, but different measures of zoobenthic community structure revealed differing levels of development. Infaunal density increased linearly during the first 2 yr (first sampling event ~4000 ind. m^{-2} ; Fig. 1e), but it later decreased, and the created marsh again showed significantly lower overall density than the natural marsh (marsh type \times time: $F_{10,60} = 2.22$, $p = 0.036$; marsh type: $F_{1,60} = 6.98$, $p = 0.038$; time: $F_{10,60} = 1.24$, $p = 0.28$). Diversity, measured as taxon richness, varied between marshes over time (marsh type \times time: $F_{10,60} = 4.13$, $p = 0.0002$;

marsh type: $F_{1,60} = 19.03$, $p = 0.005$; time: $F_{10,60} = 2.28$, $p = 0.024$). Initially (spring 1996), the created marsh had a significantly lower number of species (2.25 taxa $core^{-1}$) than the natural marsh (8.75 taxa $core^{-1}$; $p < 0.01$), but richness increased during the following 18 mo to match that of the natural marsh community. Created marsh species richness reached a relatively stable level (Fig. 1f), but when differences occurred between marshes, the natural habitat showed higher richness than the created marsh (spring 2001, $p < 0.001$; spring 2003, $p < 0.01$). Correspondingly, Shannon diversity in the created marsh increased during time (marsh type \times time: $F_{10,60} = 2.96$, $p = 0.0043$; marsh type: $F_{1,60} = 2.33$, $p = 0.18$; time: $F_{10,60} = 3.52$, $p = 0.0011$; Fig. 1g). There were differences in evenness driven by both marsh type ($F_{1,60} = 6.24$, $p = 0.015$) and time ($F_{10,60} = 2.96$, $p = 0.0039$), but with no significant interaction between the factors ($F_{10,60} = 1.43$, $p = 0.19$). The natural marsh showed lower evenness than the created marsh, indicating higher dominance of a few species in the natural marsh habitat. Evenness increased in the marshes during the study (Fig. 1h), with fall 2001 being significantly higher than fall 1996, and spring and fall 1997 ($p < 0.05$).

The composition of the infaunal community varied over time between the 2 marsh types (PERMANOVA, marsh type \times time: $F_{10,66} = 3.18$, $p \leq 0.0001$). The marshes differed significantly from each other during the first 2 yr (1996–1997), and also in fall 1998 and spring 2001 and 2003 (all $p < 0.05$). Decreasing relative density of microalgae-feeding insect larvae, such as Chironomidae and Ceratopogonidae, and increasing relative density of detritivore oligochaetes dominated the changes in the created marsh (Fig. 2).

Trophic links revealed by stable isotope tracer experiments

Through stable isotope labeling, we identified trophic linkages between 4 basal food sources and 14 consumer taxa in the salt-marsh macrofaunal community (Fig. 3). Context-dependent (marsh-specific) divergences in tracer incorporation were rare, as consumers showing uptake of label (or lack thereof) generally did so in the same manner in both marsh types (see Table S1 in the Supplement). Consequently, we present the results from both marshes together. Of the consumers that incorporated isotopic labels, some were linked to a single food source whereas others, e.g. *Polydora* sp., Cera-

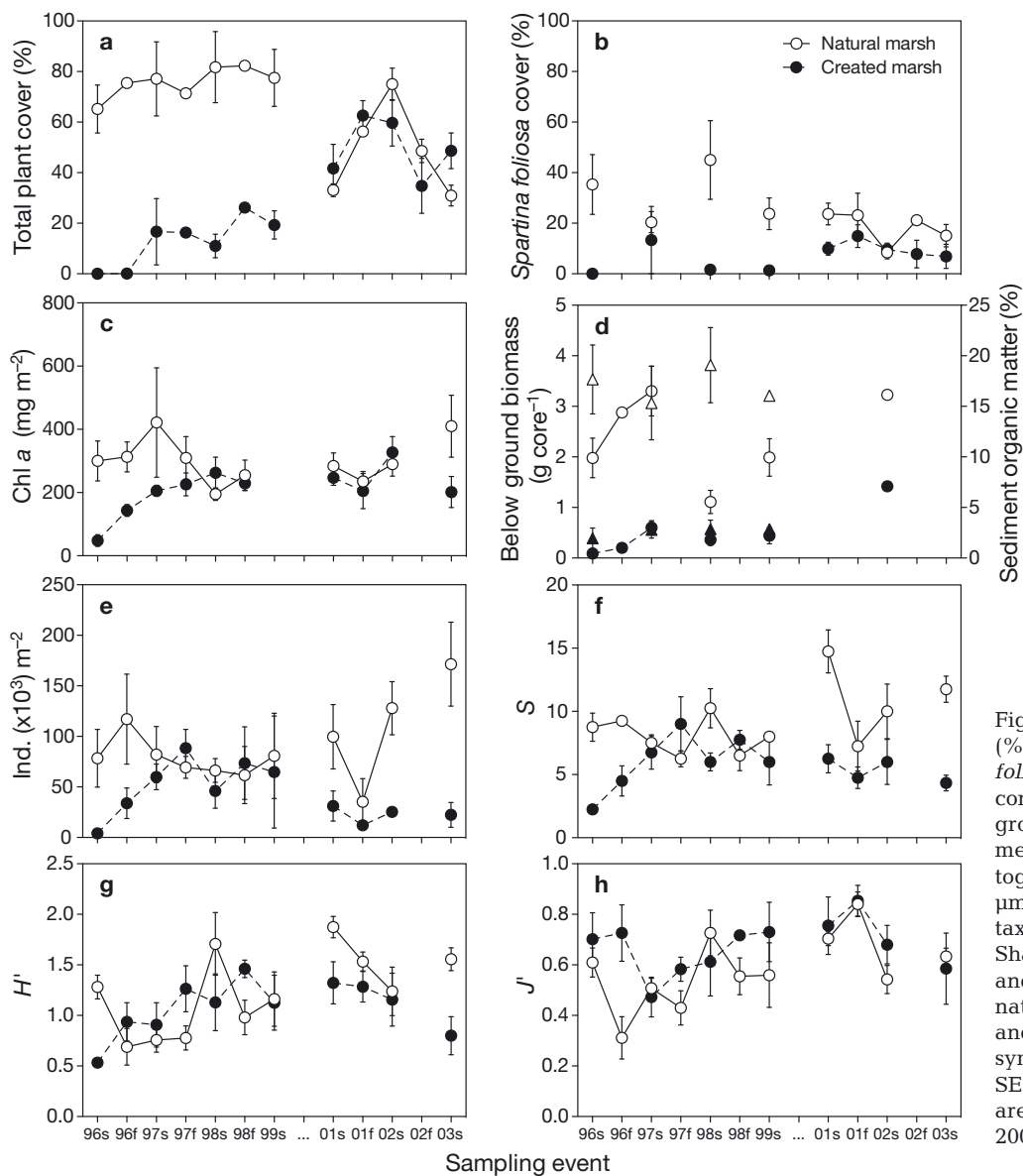


Fig. 1. (a) Total plant cover (%), (b) cover of *Spartina foliosa* (%), (c) chlorophyll *a* concentration and (d) below-ground biomass (O) and sediment organic matter (Δ); together with infaunal (>300 μm) community (e) density, (f) taxonomic richness (*S*), (g) Shannon's diversity index (H') and (h) evenness (J') in the natural marsh (open symbols) and created marsh (filled symbols). Data are means \pm SE, $n = 4$. Sampling events are given as year (1996–2003) and season (s: spring; f: fall)

topogonidae and Dolichopodidae, were connected to up to 3 basal groups. There was no obvious pattern between taxonomic group and the number of links to different food sources. Seven taxa showed ¹³C-label derived from microalgae. Very high uptake was exhibited by insects, Chironomidae, Ceratopogonidae and Dolichopodidae. The amphipod *Corophium* sp., Ceratopogonidae and Dolichopodidae also showed high utilization of N₂-fixing cyanobacteria in the created marsh. *Polydora* sp. fed selectively within the microalgae category, excluding N₂-fixing cyanobacteria from its diet.

The detrital pathway was also important, as shown by labeled bacteria and *Spartina foliosa* detritus. *Spartina foliosa* was utilized by more than half of

the consumers with recorded tracer uptake. Poduridae and *Traskorchestia traskiana* (Crustacea) were actively feeding on *S. foliosa* in the natural marsh, shown by the very high uptake of ¹⁵N by these taxa during the first days of the study (see Table S1 in the Supplement). Enchytraeid oligochaetes and the polychaetes *Polydora* sp. and *Capitella* sp. showed early enrichment from *S. foliosa*. In addition, *S. foliosa*-derived ¹⁵N was found at Day 72 in 3 insect groups and the tubificid oligochaete *Tubificoides brownae*. Invertebrates that did not show any substantial incorporation during the experiments included *Ligia* sp. (Crustacea, Isopoda), Halacaridae (Acari), *Monopylephorus rubroniveus* (Oligochaeta), Tipulidae, Muscidae (Insecta) and Nematoda.

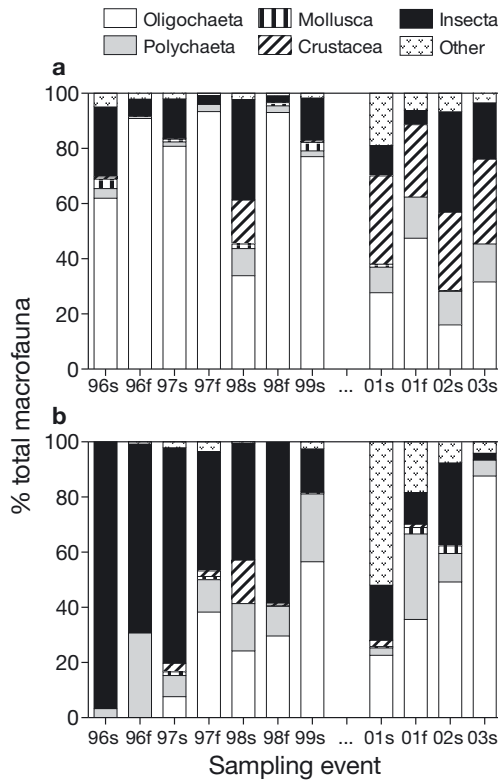


Fig. 2. Taxonomic composition of the infaunal community (n = 4 cores) in (a) natural marsh and (b) created marsh for the given year (1996–2003) and season (s: spring; f: fall)

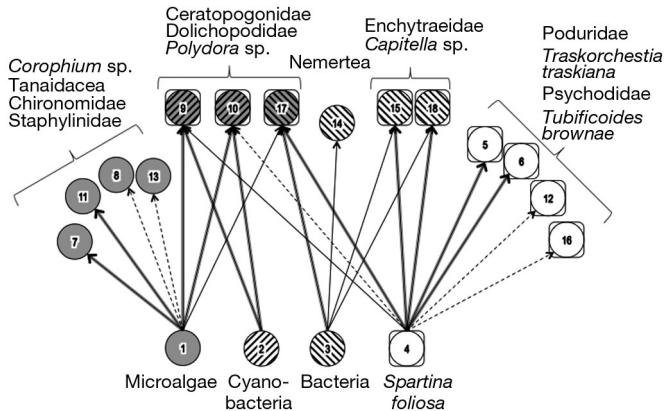


Fig. 3. Trophic links determined through isotope enrichment experiments in created and natural marsh *Spartina foliosa* vegetation. Solid arrow indicates moderate incorporation ($10\% \leq \Delta\delta^{13}C/\delta^{15}N < 25\%$), thick arrow indicates very high incorporation ($\Delta\delta^{13}C/\delta^{15}N \geq 25\%$) and dashed lines show late transfer of label. Note that lines could be direct or indirect, i.e. indicate leaching or predation. 1 = microalgae, 2 = cyanobacteria, 3 = bacteria, 4 = *Spartina foliosa*, 5 = Poduridae, 6 = *Traskorchestia traskiana*, 7 = *Corophium* sp., 8 = Tanaidacea, 9 = Ceratopogonidae, 10 = Dolichopodidae, 11 = Chironomidae, 12 = Psychodidae, 13 = Staphylinidae, 14 = Nemertea, 15 = Enchytraeidae, 16 = *Tubificoides brownae*, 17 = *Polydora* sp., and 18 = *Capitella* sp.

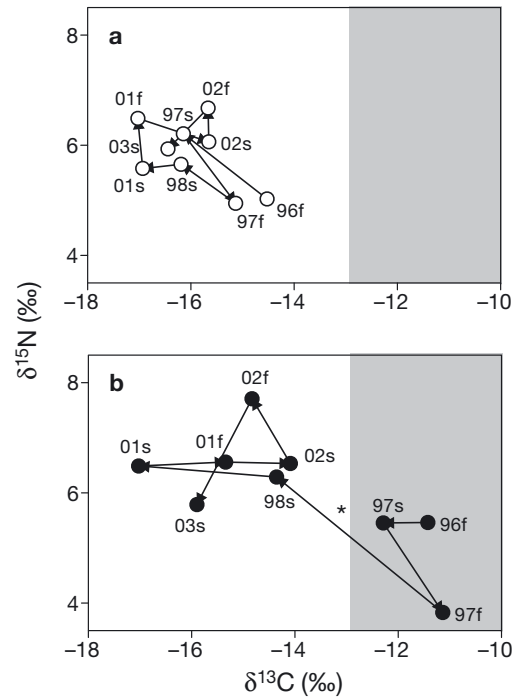


Fig. 4. Temporal path of centroid location in (a) natural and (b) created marsh, beginning in fall 1996 (96f) and ending in spring 2003 (03s). Sampling events are given as year (1996–2003) and season (s: spring; f: fall). *The fall 1997 to spring 1998 centroid shift within the created marsh was significantly different from zero (difference = 4.048, $p = 0.0001$). The gray area shows centroids of created marsh consumer assemblages that differed significantly from the corresponding assemblages in the natural marsh

Isotopic development of the salt-marsh consumer assemblage

We studied trophic succession by comparing temporal patterns of consumer stable isotopes between created and natural *Spartina foliosa* marsh communities. During the first 2 yr, the created marsh consumers were offset from the natural marsh consumers in isotope space (Fig. 4, see Fig. S2 in the Supplement). The location of the consumers varied over time in the created marsh, but the natural marsh showed no significant changes between consecutive sampling events (Fig. 4, see Table S2 in the Supplement). The created marsh location shifted after 2 yr (difference = 4.048, $p = 0.0001$), resulting in a separation of early and later created marsh consumers. The 1997–1998 shift in isotopic niche space was due to the changing $\delta^{13}C$ of the consumers, which became significantly lighter ($t_{14} = 4.99$, $p = 0.0002$). The change in $\delta^{15}N$ towards higher values was smaller and non-significant ($t_{14} = 2.10$, $p = 0.055$). The shift is

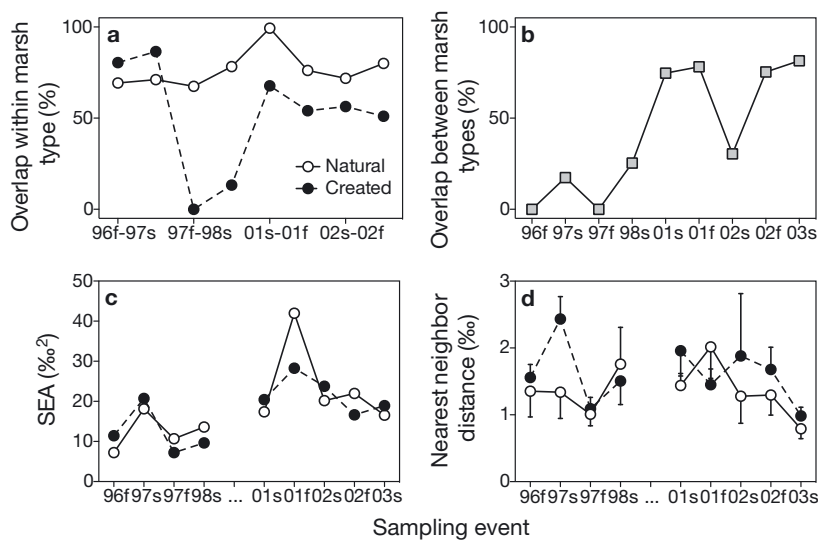


Fig. 5. Overlap (%) of marsh consumers (a) consecutively within and (b) between marsh types. Also shown are temporal changes in (c) trophic diversity measured as standard ellipse area (SEA), and (d) trophic redundancy measured as distance to nearest neighbor (means \pm SE) of salt-marsh consumers. Open symbols represent the natural marsh and filled symbols represent the created marsh. Sampling events are given as year (1996–2003) and season (s: spring; f: fall)

also seen in the patterns of assemblage overlap between sampling dates. The greatest isotopic changes (lowest overlap) occurred within the created marsh during early to intermediate years (1997–2001; Fig. 5), coinciding with the significant change in location in isotope space. The last 2 yr of the study period show higher, and more stable overlap within the created marsh, although at lower levels than before the shift.

The changes were most pronounced in the created marsh, which shifted to resemble the natural marsh. Looking at a subset of 12 taxa representing detritivores, microalgivores, omnivores, predators and primary producers, stable isotope shifts between early (1996–1998) and later (2001–2003) years occurred in random directions in the natural marsh (Rayleigh's test, $Z = 2.427$, $p = 0.086$). Created marsh taxa shifted in a uniform way, in the direction towards more depleted $\delta^{13}\text{C}$ values (Rayleigh's test, $Z = 4.557$, $p = 0.008$). Other responses were group- or species-specific, e.g. detritivore path length (96f–03s) was significantly longer (difference = 10.93, $p = 0.002$) in the created marsh than in the natural marsh, whereas path lengths did not differ between marshes for the epifaunal microalgivore *Cerithidea californica* (difference = 0.61, $p = 0.111$) or the predatory *Fundulus parvipinnis* (difference = 5.15, $p = 0.163$). However, we found no differences in overall assemblage path length (difference = 6.36, $p = 0.82$), direction ($\theta =$

10.60° , $p = 0.19$) or shape (difference = 0.51, $p = 0.19$) between the created and the natural marsh (Fig. 4).

Contrary to our expectation, the marshes did not differ in trophic diversity (Fig. 5, see Supplement 4) over time. However, there were some temporal changes in trophic diversity measured as SEA, but not when estimated as distance to centroid. The potential for trophic redundancy was relatively homogenous and did not differ between marshes or between consecutive sampling events within marsh types. Sample size or number of taxa may influence these metrics at low levels of diversity, but no significant relationships were found between the number of taxa included in the analysis and trophic diversity or redundancy (see Fig. S3 in the Supplement).

DISCUSSION

Trophic succession in the infaunal community

Our results were consistent with bottom-up, trophic-based succession of benthic community structure and food-web properties in a created salt marsh in Southern California. The created marsh exhibited a directional change over time in faunal stable isotope ratios and community composition (Fig. 6). With respect to changing vegetation complexity and food source availability, the amounts of microalgae, vascular plants and detritus increased before fauna responded. This suggests that primary producers and restored structure are closely linked to the recovery of the benthic food web. However, although the plants are the foundation of the marsh, a single structural metric (e.g. plant density) is not likely to accurately determine or predict functional restoration success because of the intricacies of marsh community succession. Plant recovery may occur in absence of animal recovery (Levin et al. 1996), and our study shows that different parts of the community reestablish at different times, at different rates and with varying degrees of recovery. For example, we expected infaunal density and diversity in the created marsh to increase over time and eventually match levels in the natural marsh. Such patterns were indeed found, but did not persist for all variables. A transient conver-

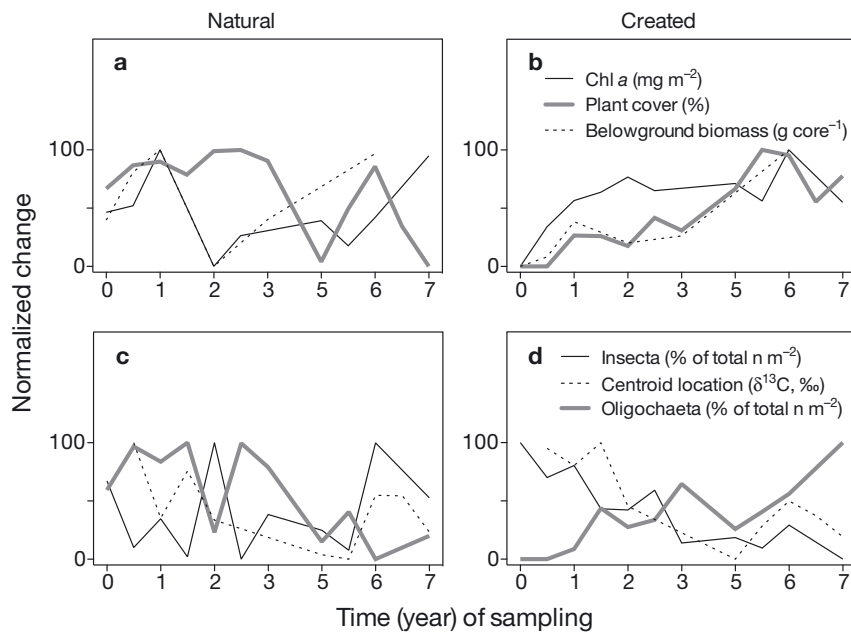


Fig. 6. Generalized temporal development of (a,b) food source and (c,d) consumer components of the natural and created marsh. All variables were normalized (0–100) prior to plotting, revealing any directionality of change. Note that the magnitude of change is not comparable between marshes. Time 0 indicates when created marsh succession was initiated

gence between created and natural marsh infaunal structure indicates an incomplete recovery of the macrofauna. In this study, some changes in the created marsh followed a major El Niño event (1997–1998), which raised effective sea level by about 10 cm and helped wet the created marsh habitat (Levin & Talley 2002). This may have temporarily increased the compositional similarity of the 2 marshes, adding polychaetes and crustaceans to the created assemblage. However, the positive El Niño influence on the system appeared to subside over subsequent years.

In the context of trophic succession, changing food source availability may entail successional changes in absolute amounts of food, a higher diversity in the functional types of food sources (microalgae versus vascular plants, grazing versus detritus pathways), and changes in the taxonomic composition of primary producers within a guild. Regarding biodiversity, vascular plant species richness positively influences above- and belowground consumer abundance, diversity and multi-trophic interactions by providing temporally consistent food and habitat (Scherber et al. 2010, Haddad et al. 2011). Sediment-dwelling macrofauna show functional shifts in response to changes in abiotic and biotic characteristics following redevelopment of marsh plant vegetation (Levin & Talley 2000, Whitcraft & Levin 2007) or invasion of, for example, hybrid *Spartina* sp. to previously unvegetated mud-

flats (Levin et al. 2006, Neira et al. 2007, Grosholz et al. 2009).

Among the food sources, the establishing microalgal assemblage characterized the earliest stage of marsh succession (Fig. 6). Although initial microalgal biomass was low, the created marsh quickly developed a consumer community dominated by surface, microalgal-feeding insect larvae able to tolerate high salinities and temperatures. Insect abundances (absolute, not relative) increased in parallel to the microalgae they grazed upon. While our data set lacks direct estimates of the composition of microalgae along the marsh successional trajectory, mixing models reveal that the cyanobacterial part of the microalgal complex is particularly important in the earliest years of marsh development, whereas marsh consumers in natural habitats rely on a greater diversity of food sources (Currin et al. 2011).

Following the initial 2 yr increase in microalgal biomass, vascular plant cover and belowground biomass continued to increase for 5 to 6 yr after marsh creation. The subsequent trophic succession in the created marsh was seen as a shift in consumer guilds to a relative dominance of subsurface-feeding detritivores (oligochaetes) (Fig. 6). Detritus contributes to food source diversity, fueling different types of microbes as it is degraded and remineralized. Fungi are key for standing-shoot decay, and bacteria become important when plant matter reaches the sediment (Newell & Porter 2000). Absolute densities of insect larvae did not differ between marsh types, indicating that food-web complexity increases as the detrital pathway is added to the trophic structure of the created marsh. Rather than a complete substitution of consumer taxa as the marsh develops, there is an expansion of the food web, with plant detritus supporting an additional set of consumers as well as generalist taxa already inhabiting the created marsh (Schrama et al. 2012). This pattern indicates an increasing trophic complexity during succession (Odum 1969, Oksanen et al. 1981, Neutel et al. 2007). Modeling work has shown that the inclusion of the detrital complex can promote food-web stability by increasing the prevalence of weak links (McCann et al. 1998) and by adding slow (detrital) energy channels to the food web (Moore et al. 2004, Rooney & McCann 2012).

Changes in consumer composition corresponding to those we observed have been reported in other Southern California salt marshes (Talley & Levin 1999, Moseman et al. 2004), and thus the system we studied (although lacking whole-marsh replicates) appears to be representative of successional wetlands in the area. In addition to these local parallels, similar successional trajectories were found in studies conducted on the US east coast (Levin et al. 1996) and in Europe (Schrama et al. 2012). The observed changes in the trophic characteristics of the community support the hypothesized food-web development, and are consistent with findings of successional shifts from fast to slow cycles, e.g. in soil food webs (Ferris & Matute 2003). Bottom-up structuring of trophic networks (Oksanen et al. 1981, Power 1992) also occurs during the successional development of grazing webs in lakes (Sommer 1985) and old fields (Siemann et al. 1999), detritus webs in forests (Chen & Wise 1999) and soils of sand dunes (Neutel et al. 2007). Thereby, bottom-up forces influence community functioning and stability in a range of systems. Successional changes in primary producer availability, structural complexity and carbon dynamics are likely to affect the relative importance of, and linkages between, grazer and decomposer food webs.

Community development in isotope space

Surprisingly, we did not find evidence that succession influences trophic diversity or redundancy in isotope space. This may be due to the qualitative nature of the metrics, which were based on averages for taxa and were not weighted by abundance or biomass. Also, the salt-marsh system is dominated by fewer species with broader diets rather than more highly specialized taxa (Teal 1962). However, the increasing overlap and evident convergence between the natural and created marsh consumer isotope signatures support the hypothesis of trophic/basal food-source succession: isotopic similarity increases as the created marsh community develops. Corresponding changes in isotope signatures in developing salt marshes have been found for individual species of epi- and infaunal macroinvertebrates (Moseman et al. 2004, Howe & Simenstad 2007), fish (Wozniak et al. 2006), as well as an arthropod community following restoration that involved removal of *Phragmites australis* (Gratton & Denno 2006).

Changes in consumer assemblage isotopic signatures can occur through changes in consumer com-

position, consumers switching diets, and/or food sources changing stable isotope ratios. There were clear changes in consumer assemblage composition during marsh succession, but the core group of taxa sampled for stable isotope analysis remained relatively stable over time. Furthermore, the taxa in the created marsh showed parallel changes towards lighter C isotopes, suggesting, for example decreased utilization of N₂-fixing cyanobacteria with marsh development (see Currin et al. 2011 for mixing models). In addition, changes in the C isotope composition of microalgae over time may have contributed to changes in consumer values. Although marsh vascular plants and macroalgae, such as *Spartina foliosa*, *Sarcocornia pacifica* and *Ulva* spp., did not differ in $\delta^{13}\text{C}$ between marshes, microalgae in the absence of shade or plant structure show higher $\delta^{13}\text{C}$ values (Whitcraft & Levin 2007, Currin et al. 2011). Higher $\delta^{13}\text{C}$ values suggest increased photosynthetic rates and associated carbon limitation, higher salinity, or reduced utilization of remineralized plant matter (Beardall et al. 1998, Raven et al. 2002). The developing plant canopy and associated changes in sediment abiotic conditions (reduced irradiance with lower temperature and porewater salinity) (Levin & Talley 2002, Whitcraft & Levin 2007) may lower $\delta^{13}\text{C}$ values of the microalgal community, which are tracked by the invertebrate consumers (Wozniak et al. 2006, Whitcraft & Levin 2007), potentially generating the patterns seen in our study.

Use of stable isotopes in tracking recovery following disturbance

The food web constitutes the framework within which the effects of both abiotic and biotic processes are manifested (Polis & Winemiller 1996), and is, as a concept and tool, suitable to significantly advance the understanding of interrelationships between community structure and ecosystem functioning in the face of environmental change and disturbance (Sala & Sugihara 2005). Stable isotopes offer multiple insights about food webs, as tracers of C and N, for trophic level assessments, and as proxies for trophic structuring within species and within whole assemblages, including bottom-up and top-down forcing (Vander Zanden et al. 1999, Layman et al. 2012). Stable isotope approaches can thereby be useful for monitoring changes in community trophic interactions under different management scenarios or strategies, including ecological restoration (Gratton & Denno 2006). Establishing rates of recovery of

trophic structure or diversity can help determine monitoring strategies and success criteria for restoration. The identification of primary producer taxa or guilds driving recovery may further guide practices, such as planting, fertilizing, tilling or adding of detritus to speed up restoration. The method also enables identification of baseline/benchmark functioning of a system against which future changes, such as those due to climate change, can be assessed. For example, changing conditions such as increased CO₂ levels, higher temperatures and different precipitation patterns may alter the availability of primary producers, their quality or their use by consumers.

The isotope enrichment approach helps pinpoint feeding links in a rapid and often unambiguous way (Herman et al. 2000). Although we did not find habitat-dependent trophic linkages, the feeding links differed among consumer taxa and helped us identify the trophic consequences of a changing consumer community. We note, however, that uptake of labeled C or N may occur through processes other than direct consumption of the labeled food source. Label incorporation could result from predation on organisms one or more trophic levels removed from the labeled primary producer. Alternatively, label may leach from primary producer tissue, or enter the dissolved pool through remineralization and become incorporated by other primary producers or bacteria. Nevertheless, the transfer of C or N from the original source to consumers took place rapidly and provides direct evidence of C and N assimilation derived from specific food sources. Over longer periods, multiple indirect pathways may make interpretation of label transfer difficult. Used in combination, natural abundance data and stable isotope enrichments can enhance food-web interpretation and broaden our understanding of dynamic trophic succession. Succession is not necessarily a linear process (Zedler & Lindig-Cisneros 2000), and different measures of system development may be required to assess all temporal phases. To the extent that recovery after disturbance involves matched patterns of trophic diversity and functional redundancy between developing and reference systems, isotope metrics and trajectories may be a useful tool. However, our results show that isotope metrics (e.g. Fig. 5c,d) can conceal composition or feeding-group differences (Figs. 2 & 4) that may reflect altered ecosystem function, thus highlighting the need for complementary metrics in assessments of trophic structure in complex communities.

As larger-scale environmental conditions are the same for both the created and the natural marsh, the development in the benthic community and the food

web can mainly be attributed to factors other than specific site characteristics, such as trophic succession, plant–animal interactions including facilitation, or top-down mechanisms. Although several aspects of our study link macrofaunal succession to changes in the basal part of the food web, we cannot assume that bottom-up processes exclusively shape community structure (Chase et al. 2000, Silliman & Bertness 2002). However, our results are consistent with trophic succession for assemblages of small (0.3–1 mm) animals, whereas larger epifauna and nekton in the system are yet to be explored. In conclusion, we identify resource-mediated succession in Southern California wetlands, in which comparable lower trophic-level food webs reestablish quickly.

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The following supplement accompanies the article

Benthic food-web succession in a developing salt marsh

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Supplement. Additional site information and isotopic analysis data

Study site

The Mission Bay marshes (Fig. S1) are subject to California's mixed semidiurnal tidal regime with 2 high and 2 low tides (of differing amplitude) each day. Additionally, there are weekly and seasonal patterns of greater (2 sets, spring) and lesser (2 sets, neap) amplitude tides per lunar cycle, and greatest tidal amplitudes around the December and June equinoxes. Our sampling was concentrated to intertidal, low-marsh habitats dominated by *Spartina foliosa*.

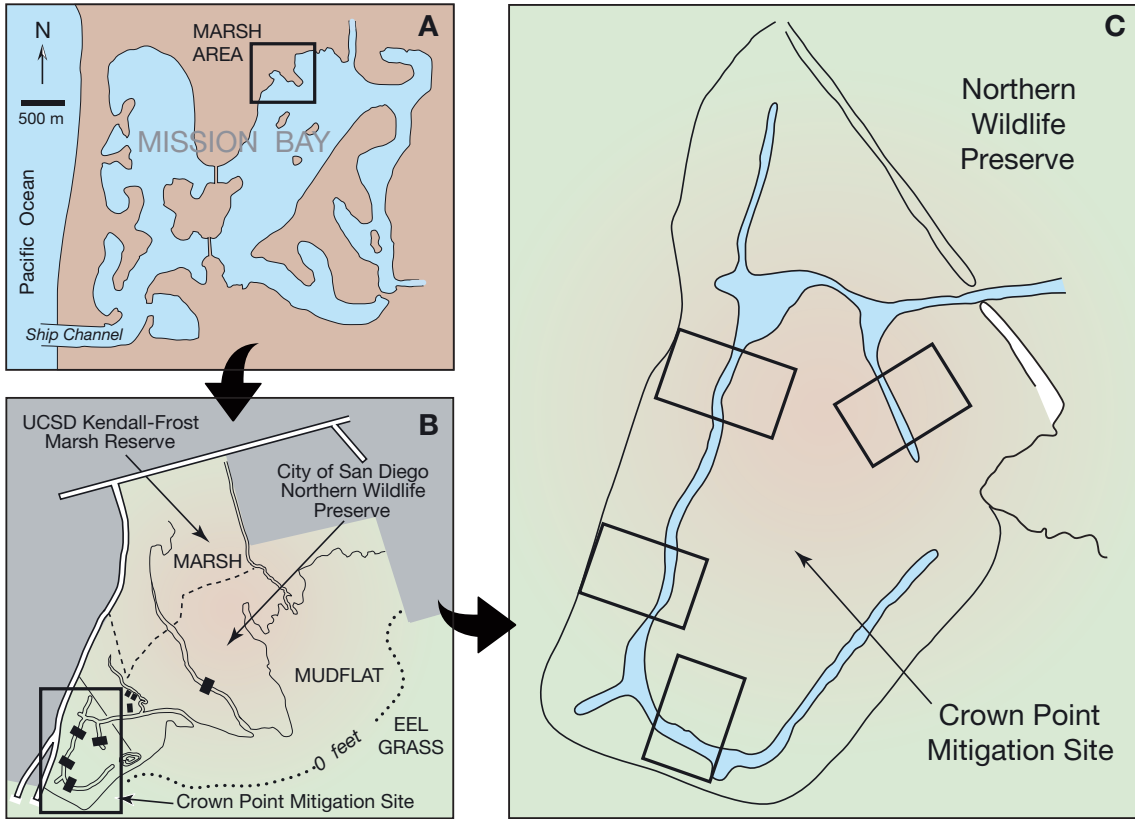


Fig. S1. (A) Location of the Crown Point Mitigation Site (created in December 1995) and the adjacent natural marsh (Northern Wildlife Preserve) in Mission Bay, San Diego, CA. (B) Black rectangles show 4 sampling plots in the natural marsh and in the created marsh, with (C) a close-up of the latter (modified from Currin et al. 2011).

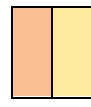


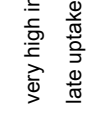
Isotope sample collection and processing

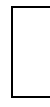
Primary producers and consumers in the natural and the developing marsh were collected, pretreated and analyzed for natural abundances of carbon and nitrogen stable isotope ratios as described in Currin et al. (2011). In brief, we collected infaunal invertebrates by coring, and epifauna, macroalgae and plants by hand. Fishes were collected in marsh creeks using unbaited minnow traps and throw nets. The infauna were sorted live, identified and stored in filtered seawater (<25 μm) overnight to allow for clearance of guts. Samples were acidified (1 N HCl) for removal of carbonates. Fishes (Fundulidae, Gobiidae) and epifauna (Gastropoda, Bivalvia, Decapoda) were dissected for muscle tissue. Samples consisted of a single individual, unless pooling of several individuals was necessary to achieve required sample mass.

Stable isotope ratios (^{13}C , ^{12}C or ^{15}N , ^{14}N) were expressed relative to international standards (V-PDB for carbon and atmospheric N_2 for nitrogen) using δ notation, e.g. $\delta^{13}\text{C}_{\text{sample}} (\text{‰}) = [({}^{13}\text{C}/{}^{12}\text{C}_{\text{sample}})/({}^{13}\text{C}/{}^{12}\text{C}_{\text{standard}})-1] \times 10^3$. The corresponding analysis was conducted on primary producers and consumers collected during the stable isotope enrichment experiments (Table S1).

Table S1. Trophic links to marsh consumers identified during stable isotope enrichment experiments. Maximum and, within parentheses, mean incorporation of stable isotope labels are shown. Values in brackets show late incorporation with no early samples (t_{24} - t_{144}) available

Taxa, trophic group	2001		2002		2002		2002		2002	
	Microalgae		Microalgae		Cyanobacteria		Bacteria		Spartina foliosa	
	Natural	Created	Natural	Created	Natural	Created	Natural	Created	Natural	Created
Poduridae							4 (3)		100 (54)	
<i>Orchesia traskiana</i>							-2		154	
<i>Corophium</i> sp.		26 (17)								
Tanaidacea		[12]								
Ceratopogonidae	15 (9)	61 (32)	13	79 (78)	[11]	118 (59)		8 (7)	[11]	14 (13)
Dolichopodidae		2		61		75		8 (5)	[25]	9 (7)
Chironomidae	26 (13)	46								
Psychodidae	0								[39]	
Staphylinidae				[11]		1				
Nemertea		4		7		1		-6	14	0
Enchytraeidae	2	1	0		4			15 (10)		
<i>Tubificoides brownae</i>										
<i>Polydora</i> sp.		13 (8)		14		-3			49 (26)	28 (20)
<i>Capitella</i> sp.	-2	8 (4)							19 (12)	42 (28)

 no/negligible moderate incorporation, <10%
 moderate incorporation, ≥10%
 very high incorporation, ≥25%
 late uptake

 No data available for trial/no late uptake

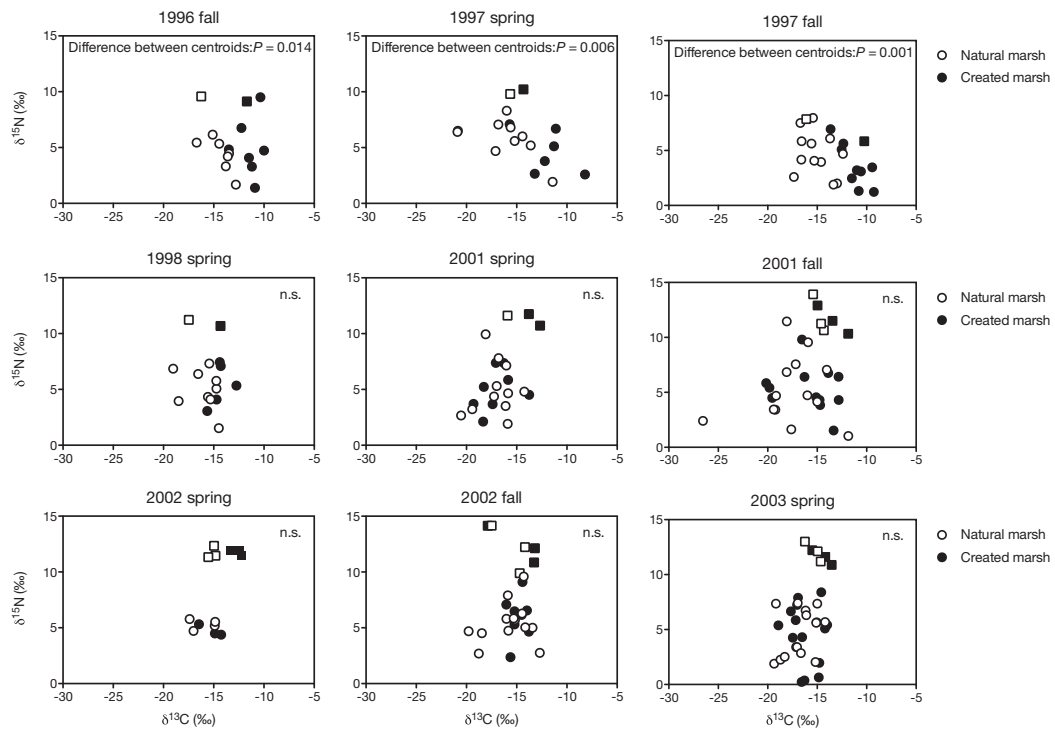


Fig. S2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($n = 6\text{--}18$) of consumers in natural and created *Spartina foliosa* marshes. Circles indicate macroinvertebrates and squares indicate fishes. Each point represents the mean value for a particular taxon. The consumer assemblage positions in isotope space differed (residual permutation procedure) during the first 2 yr of the developing marsh (top 3 panels)

Table S2. Comparison of isotopic niche properties (centroid location, mean distance to centroid, mean distance to nearest neighbor, and difference between standard ellipse area [SEA]) (A) within the mature marsh, (B) within the young marsh and (C) between marsh types. Absolute distances and differences significantly different from zero shown in bold. S: spring; F: fall

		Centroid location		Distance to centroid		Nearest neighbor		SEA
		Distance	p	Difference	p	Difference	p	p
(A) Natural marsh								
1996 F	vs. 1997 S	2.008	0.144	0.716	0.373	0.016	0.980	0.034
1997 S	vs. 1997 F	1.619	0.170	0.475	0.440	0.330	0.366	0.879
1997 F	vs. 1998 S	1.272	0.288	0.172	0.751	0.749	0.059	0.668
1998 S	vs. 2001 S	0.747	0.734	0.372	0.619	0.320	0.448	0.746
2001 S	vs. 2001 F	0.911	0.754	1.491	0.086	0.577	0.371	0.008
2001 F	vs. 2002 S	1.437	0.623	0.252	0.811	0.735	0.428	0.032
2002 S	vs. 2002 F	0.615	0.858	0.956	0.324	0.016	0.984	0.647
2002 F	vs. 2003 F	1.076	0.477	0.045	0.950	0.504	0.103	0.768
(B) Created marsh								
1996 F	vs. 1997 S	0.864	0.758	0.445	0.567	0.874	0.195	0.832
1997 S	vs. 1997 F	1.991	0.146	0.978	0.166	1.342	0.008	0.037
1997 F	vs. 1998 S	4.048	<0.001	0.250	0.695	0.416	0.506	0.632
1998 S	vs. 2001 S	2.511	0.240	1.427	0.261	0.452	0.603	0.945
2001 S	vs. 2001 F	1.789	0.332	0.062	0.938	0.507	0.418	0.813
2001 F	vs. 2002 S	1.252	0.692	1.123	0.250	0.430	0.671	0.740
2002 S	vs. 2002 F	1.390	0.590	1.761	0.149	0.202	0.855	0.719
2002 F	vs. 2003 F	2.199	0.122	0.443	0.563	0.697	0.188	0.695
(C) Natural versus created marsh								
1996 F		3.129	0.01	0.515	0.477	0.205	0.616	0.770
1997 S		3.927	0.003	0.243	0.770	1.095	0.116	0.502
1997 F		4.147	<0.001	0.259	0.546	0.082	0.806	0.824
1998 S		1.938	0.190	0.181	0.833	0.250	0.746	0.787
2001 S		0.280	0.965	0.873	0.348	0.521	0.419	0.656
2001 F		1.689	0.359	0.679	0.388	0.563	0.289	0.873
2002 S		1.636	0.567	0.695	0.601	0.602	0.437	0.578
2002 F		1.328	0.422	0.109	0.907	0.384	0.406	0.806
2003 f		0.566	0.777	0.288	0.645	0.191	0.376	0.640

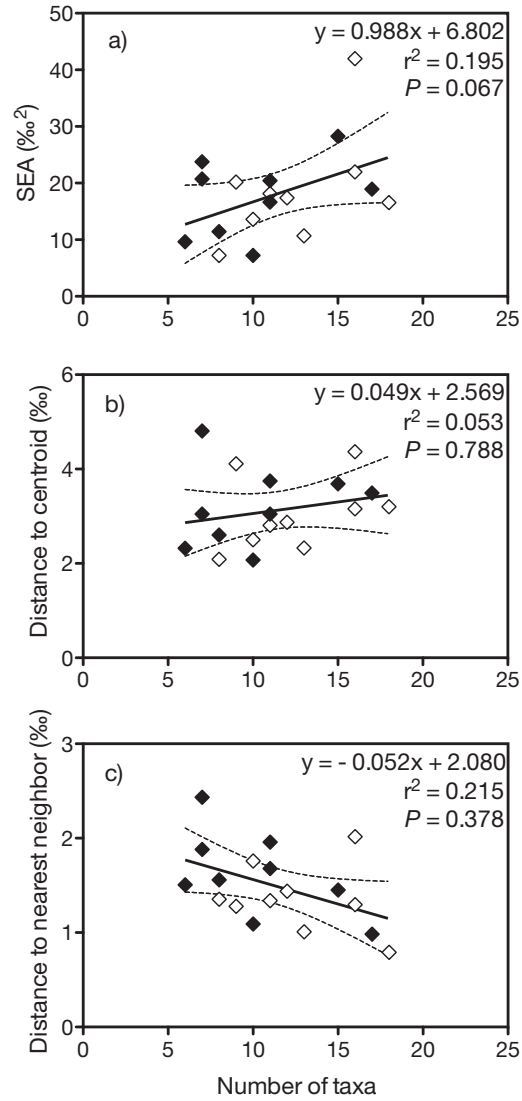


Fig. S3. The relationship between number of taxa included in the analyses and (a) standard ellipse area (SEA), (b) distance to centroid and (c) distance to nearest neighbor for each sampling date as a function of marsh type. Lines show slope with 95% confidence intervals from linear regression. Open symbols represent the natural marsh and closed symbols represent the created marsh