Salt Marsh Secrets

Who uncovered them and how?

By Joy B. Zedler

An e-book about southern California coastal wetlands for readers who want to learn while exploring

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This e-book records favorite stories about salt marsh secrets that my collaborators and I uncovered while studying southern California coastal wetlands, from the 1970s to date. In 1986, we became the Pacific Estuarine Research Lab.

Please download the files as they appear online and enjoy learning what we learned…and more. You'll meet many "detectives," and you'll be able to appreciate how they learned so much--undeterred by mud and flood. Learn while exploring the salt marshes near you!

Each chapter (1-21) is being posted at the TRNERR as a separate file (PDF).
Chapter numbers precede page numbers (for chapter 1: 1.1...1.14).
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PDF name and brief description:

Restoration

If you wreck your car, professionals can usually put it back together so that it looks like new *and* runs like new. They might need to consult various "how to repair" books or they might need to ask for help from another expert who knows your car model inside and out. They also might need to order replacement parts or go prospecting in the local vehicle graveyard, looking for an undamaged hood or motor from an identical or similar vehicle that someone discarded. Those simple actions—reading how to repair it and finding replacement parts—represent a century of knowledge accumulated by car-repair professionals, involving vocational schools, training programs, parts-supply warehouses and distribution systems, tool manufacturing and distribution, vehicle junkyards and mechanics who rehabilitate used parts.

(millsmotors.com)

If pros can restore cars, can we professional ecosystem restorationists do the same for damaged salt marshes? Do we have the same resources available to us as in "car rehab"? Which critical parts are missing for ecosystem restoration? You'll see some shortcomings in the right-hand column below:

The auto-repair profession has	The ecosystem restoration profession has:
Vocational schools	Universities
Many how-to books, including books for specific vehicle models	Few general how-to books, relative to the diversity of ecosystems needing repair
Training programs, apprenticeships	Restoration ecology courses; volunteer opportunities, internships, hands-on experience
Parts-suppliers and distribution systems	Nurseries, native gardens
Tool manufacturing and distribution	Equipment and tools borrowed from agriculture, horticulture, forestry, etc.
Vehicle junkyards	Few remnants of native ecosystems for seed collection
Used-part rehabilitators	Rare opportunities to salvage plants, soil, etc.
Not applicable	Inability to restore an ecosystem's watershed
Not applicable	Inability to restore species throughout their biogeographic regions
Payment by the vehicle owner and insurance company	Limited time, personnel and money for restoration projects
Unused & fully-restored cars of the same model	Elusive reference systems, meaning they are hard to find.

What's a good reference ecosystem?

Every study of ecosystem disturbance and every plan for restoration can benefit from comparative information from "reference ecosystems." Reference ecosystems are places in the same region that are the least disturbed examples of the ecosystem under study. For southern California salt marshes, we found the least disturbed salt marshes along the edge of San Quintín Bay in Baja California Norte. There were diverse plants and animals, few roads, and little evidence of human impacts.

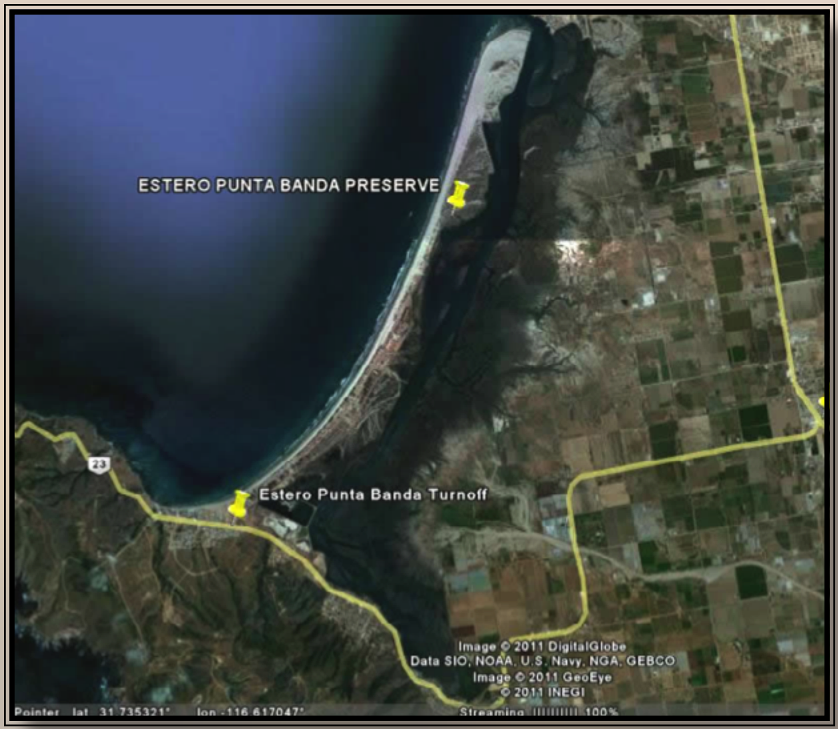
(http://www.bestbajafishing.org/img/san-quintín.jpg)

The salt marsh west of Ensenada in Estero de Punta Banda also provided helpful data. In both Mexican reference ecosystems, Dra. Silvia Ibarra-Obando, from the *Centro de Investigación Cientí ica y de Educación Superior de Ensenada, called CICESE,* was our local expert. Silvia and her graduate student, Miriam Poumian-Tapia conducted long-term research in Estero de Punta Banda. Silvia also provided knowledge and advice based on her expertise on seagrasses (the topic of her dissertation) in Baja California. Silvia has been a friend and professional colleague throughout my career. Our visits to Baja California gave SDSU students experience with near-pristine wetlands. The salt marshes were in stark contrast with salt marshes in Upper California.

Silvia took advantage of a unique opportunity to document changes in part of Estero de Punta Banda, where a new dike was being built to create a nontidal basin. Tidal flushing was being excluded so that a developer could trap sea water and build floating oil-drilling platforms for later transport offshore. That project was abandoned, but the dike remained, and the non-tidal water and soil became hypersaline, leaving a degraded salt marsh as its legacy.

Silvia and Miriam uncovered many secrets while monitoring salt marsh vegetation. Their early findings proved extremely valuable, because the year they began sampling (1984) was the same year that Tijuana Estuary experienced tidal closure.

In both non-tidal marshes, several salt marsh plant populations declined. What caused the mortality? Was it lack of tidal flushing or some coincidental weather phenomenon? Because Silvia had comparable data for salt marshes with and without tidal flushing, her findings added credibility to our data comparing salt marsh vegetation before and after tidal flushing was excluded. The combination of Before/After and Control/Impact comparisons gave powerful evidence that mortality was caused by tidal exclusion.



(http://www.lasecomujeres.org/plants/punta_banda01.html)
The diked area is the southwestern corner of Estero Punta Banda.

Dr. Craig Osenberg developed a more elaborate "BACI" approach to assess impacts of hot-water effluent on marine organisms from the nuclear generating plant at Agua Hedionda Lagoon.

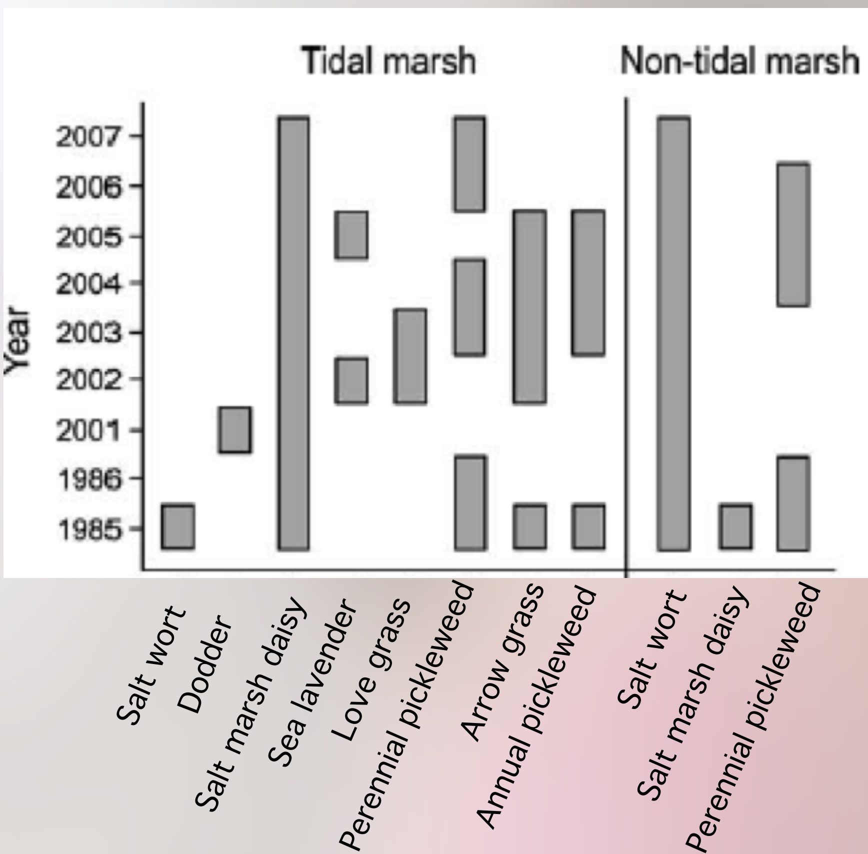
Silvia documented rates of mortality for each halophyte deprived of tides. Can you guess which species persisted the longest in the hot sun with no rain and no tidal influence? Their key findings are on the next page.

Silvia and Miriam used the same method as we used (circular 0.25-m^2 plots along transects, plus soil salinity samples). They sampled the diked and natural marshes monthly. Thanks to Silvia for having the foresight to collect comparable data! Her papers added substantial scientific understanding of the effects of tidal exclusion. The patterns for tidal versus nontidal conditions were the same as what we saw in Tijuana Estuary before versus after mouth closure.

From 1984-1986, following diking of the salt marsh that eliminated tidal influence:

- The soil salinity increased as soil moisture decreased.
- Cordgrass experienced high mortality.
- Annual and short-lived species were rapidly extirpated.
- The marsh plain shifted to dominance by perennial pickleweed, salt wort, and alkali heath.

See details in (Ibarra-Obando and Poumian-Tapia1991; also chapter thirteen of this e-book.



Over time, the dominant species shifted, with only three species remaining as "major players" in the nontidal marsh (Ibarra-Obando et al. 2010).

Dominance was calculated objectively using cover, species suppression, and tendency toward high cover (Frieswyk et al. 2007).

Salt marshes in Baja California are good reference ecosystems for restoration

The tidal portion of Estero Punta Banda is diverse and similar in composition to the Volcano Marsh that we sampled in San Quintín Bay. I don't recall the date of my first visit to Bahia de San Quintín, but it was very special to see places so free of urban impacts. Over the years, however, our field expeditions to San Quintín Bay revealed increasing impacts of humans on the wetlands.

We were part of the problem, too. We drove on upland roads to the west of Volcano Marsh, and each vehicle created a dust storm that released sediment into the strong winds that blew east, into the salt marsh. Fields where agriculture had been attempted in wetter years had the same effect. Dry soil and relentless winds took their toll on topsoil, gradually transporting it into the marshes and bay.

Later, it was increasingly difficult for me to watch the filling along the wetland edge and to observe the disregard for the land. It was easy to identify the reasons, however. Tourists from the US had money to spend, and they wanted places to camp and boat access for fishing. Salt marshes were less valued than campgrounds and boat ramps. Deepwater fishing was more attractive and profitable than mudflat clamming. We always camped at a small motel that was powered by a generator, had water brought in by truck, and offered rooms and space to camp and build a campfires. I have not returned to see how much it has changed.

Restoration plans versus outcomes

Knowing what a pristine salt marsh looks like does not guarantee that anyone can restore a degraded marsh to look and function like any reference site.

Cordgrass was planted in the Connector Marsh along east San Diego Bay (above) to provide nesting habitat for the endanergered rail (see chapter three). Above, you can see that the slope was rather steep. Planting across the range of elevations was a good strategy to find the most suitable environmental conditions. Unfortunately, a photo several years later (from the opposite direction) shows that the entire slope was lost to erosion. Elevation and slope were not the only important factors--tidal currents were also critical. The deep, wide channels that were excavated during salt marsh construction allowed strong tidal flows to erode the unstable sediment.

The edges of the eight islands also eroded, and the cordgrass that was planted around each island also eroded. In the next photo, it is easy to see that the islands provided only a narrow strip of low-elevation habitat for cordgrass.

Connector Marsh islands had "bald" spots where the soil was dense and hypersaline. We also saw broken glass, perhaps because part of this site was once a land fill (dump). We never saw bald mounds in reference wetlands, although there are natural bare salt flats in the transition to upland. Bald mounds were another signal that the restoration site had unusual substrate.

How can restoration projects be planned and implemented to persist in the long term? Hydrologists can calculate tidal flows and predict soil erosion based on slopes and elevations and soil types, but many biological components are usually left out of the models.

How might burrowing animals destabilize a channel bank? How might people trample the vegetation and reduce the ability of roots to stabilize the soil? How might a really sand soil prevent cordgrass plantings from achieving their potential to stabilize soil? By being unable to hold enough nitrogen to support vigorous growth.

How a reference marsh aids restoration

The best model for a restoration site is a natural marsh with surroundings that are similar, especially its hydrological conditions (natural flows of water from the tides and the watershed). Such a match is rare. So restorationists extrapolate (predict beyond the data), based on a reference marsh that is less disturbed than the restoration site. Volcano Marsh has served as such a model for various salt marsh restoration efforts. It has vegetation similar to that in southern California.

Drs. Gary Sullivan and John Callaway laid out transects across Volcano Marsh and surveyed elevations for us to sample with our standard 0.25-m^2 circular plots. As a result, we identified the separate effects of elevation from "proximity to the bay." Cordgrass did not occur at all elevations that seemed suitable across the marsh. It only occurred near the bay.

In planning a salt marsh restoration, it saves time and money to know the "secrets" about species distributions in relation to both elevation and degree of tidal influence. Contrast the steep-sloped islands of the Connector Marsh with the cordgrass marsh at Volcano Island in the next photo.

Cordgrass adjacent to a channel and a mudflat at Volcano Marsh.

Restorationists can now be guided to plant cordgrass near tidal embayments. Here's why: Low elevations near the bay are inundated daily by high tides, but the same elevation further inland experiences a delay—if inundated at all--during a high tide. Wouldn't it be great to have water depth indicators across the marsh so tide flows could be characterized in detail? Nowadays, affordable sensors (pressure transducers) can do this. More data would be useful!

Here's more advice: Restorationists should expect plant species to overlap, even though predicted tidal regimes imply discrete zones. Actual data on distributions show lots of overlap among species and few abrupt boundaries. Planting species across a broad range of elevations is one way to hedge bets against topographic and hydrological conditions that might have secret effects.

Our early studies provide reference data about relatively undisturbed salt marshes before major disruptions, including land use, shoreline filling and development, watershed development, climate change and increased rates of sea level rise.

Can restorationists repair both diversity and performance of degraded marshes?

Early restoration ecologists considered that ecosystems develop from having few species and low levels of functioning toward having many species and greater levels of functions. That conceptual model originated in the 1980s from Dr. Tony Bradshaw, whom I consider to be the "father of restoration ecology."

Bradshaw described ecosystem degradation as the shift from many species with high levels of function toward few species with few functions. Restoration was the reverse: human efforts to shift few species with few functions to many species with many functions. There's a huge cause → effect assumption in that model, that diversity → function. More recently, this has been rejected for wetlands (see chapter nineteen; also Doherty et al. 2014, Doherty and Zedler 2014).

Which do you think is more difficult—making a degraded salt marsh *as diverse as* a natural one or getting it to perform as it once did? Restoring diversity and function are both difficult, and the outcome probably depends on the answers to other questions. Is structure restored while some functions are not? Recall Abby Powell's study of Belding's Savannah sparrows (chapter fifteen)—the marsh appeared suitable to people and to the birds that set up territories, but the birds' nests weren't fledging many young.

In a different situation, below, you can read how nitrogen-fixation was lower in a restored marsh than in the adjacent natural wetland. N-fixation was not a function that we could see, but we could see the shorter cordgrass where less N_2 was being fixed into useful forms that plants could take up.

Were the ecosystem functions restored but not the natural structure (diversity)? Often it is possible to restore tidal flushing, but often with channels that are straight and river mouths that were armored with concrete and riprap. In other cases, salt marshes were invaded by aggressive weeds. Even if only weeds will grow, the marsh might still trap and store sediments from upstream urban or agricultural runoff (a function being performed by an unnatural structure).

In some cases, the functions of a degraded marsh are so important that restoration of a more natural structure is not a good idea. A cordgrass marsh that accumulates so much sediment that it yields dominance to perennial pickleweed will continue to have high productivity (a function), but its appearance (lost cordgrass) might not be restorable. Managers could use bulldozers to remove sediment, but that would not be permitted if the endangered Belding's Savannah sparrow has taken up residence in the pickleweed.

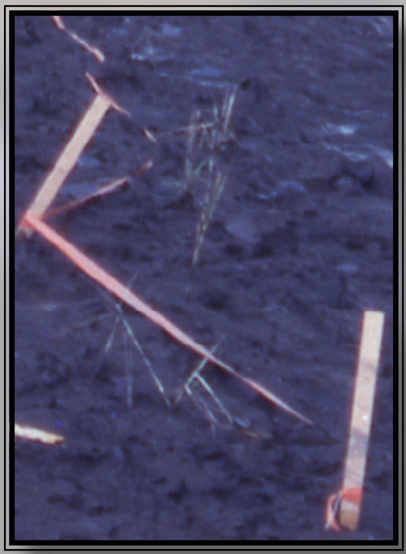
In the very long term, rising sea level might restore deeper water that can support more diverse vegetation, including cordgrass. It would be prudent to wait and see. In still other cases, the salt marsh might be so degraded that repairs are not affordable or no longer possible. The dredge spoil wetlands of San Diego Bay's Sweetwater Marsh are possible examples. Still, even the dredge spoil deposits in San Diego Bay (e.g., D-Street Fill) attract the endangered California least tern to nest.

I consider that "regional restoration" has an important role in conservation—by that I mean that we should consider all opportunities to recover native species in their historical biogeographic region, even if that opportunity is not in the exact site where the declining species once thrived. We have lost too many options for restoring all species where they once lived. What do you think?

What should restorationists do?

Each project is unique, but all projects benefit from having clear objectives, continual monitoring, and a long commitment to learn what is lacking. Where monitoring data show that a problem is developing, a "mid-course correction" might fix it. Based on a long-term study of San Diego Bay, we now understand why tall cordgrass was not restorable on the dredge spoils of Sweetwater Marsh, even after a decade of trying….

Kendra Swift laid the groundwork for our comparison of restored (excavated or constructed) and natural salt marshes of Sweetwater Marsh. In 1987, she began sampling elevations and distributions of natural cordgrass and cordgrass that CalTrans had planted as large plugs (propagated vegetatively off the site).



Cordgrass was the restoration target, because CalTrans had to replace nesting habitat for the endangered light-footed clapper rail (see chapter three). The Fish and Wildlife Service required 7 home ranges (each 2.5 acres) including nesting habitat (tall cordgrass). To identify the specific intertidal elevations with the most robust cordgrass, Kendra first identified elevation contours with maximum cordgrass cover. In July 1987, Kendra located a subset of plots with low, medium, and high cover. She measured height in July, when Ted Winfield (1980) had found the most cordgrass biomass. At replicate points, she placed a circular 0.25-m^2 plot frame and measured the stretched height of every stem in each plot, then calculated the total stem length (TSL). At the same time, she collected soil samples to measure soil texture, organic matter, and interstitial soil salinity.

Kendra found that the natural marsh soil was clay loam, and the constructed marsh soil was coarser, with less clay and more sand or silt. Organic matter was about twice as high in the natural marsh, and cordgrass was more extensive, more dense and more uniform. Surface soils were nearly always hypersaline (above 34 ppt), but salinity did not explain any aspect of cordgrass growth that she measured. July soil salinity was between 30 and 46 parts per thousand (3.0-4.6%), with the low values occurring after rainfall in November. Later, through long-term monitoring, we learned that soil salinity was greatly reduced by river flooding. We also learned that floodwaters, including nutrients, stimulated cordgrass growth.

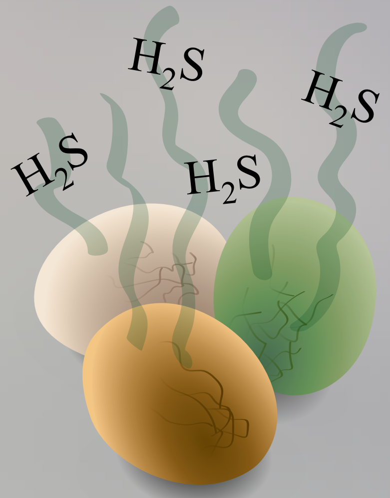
Why were the Connector Marsh soils sandy?

The eight intertidal islands were excavated from old spoils that came from dredging shipping channels in San Diego Bay. The dredged sediment was sandy. Recall from earlier chapters that natural salt marshes form on fine soils that accrete where there is little wave action, for example, inside sheltered bays like San Diego Bay.

Fine-particle soil allows marsh vegetation to establish, develop and thrive. We revealed that secret and a related question popped up: *Why* don't marshes grow well on sand? Our long-term experiments showed that the nitrogen that marsh plant roots need was not abundant, because sand particles had little ability to "hold onto" nitrate (NO_3^-) and ammonium (NH_4^+). In contrast, a fine-clay particle from a natural marsh soil is negatively charged and has high surface area per volume compared to a sand grain. Each clay particle can hold onto NH_4^+ with a weak bond (negative charge attracts the positive charge of NH_4^+). Clay soil in natural marshes provides more nitrogen, especially in the form of NH_4^+, for cordgrass to grow tall.

Kendra measured elevation with our auto-level (see chapter one). And because the nearby freeway had reference elevation markers, she could determine absolute elevation above Mean Sea Level. Kendra's work showed that where water-control structures raised the water level, cordgrass responded by growing best at a higher elevation compared to places where tides were not constrained. She also documented a problem that is common in urban wetlands—they accumulate floating trash that can smother and damage plantings. Kendra received her MS degree, and new students continued her initial comparison of restored and natural marshes.

What about sulfur?



Ever wonder why wetland sediments sometimes stink like rotten eggs? Phew! It's due to the "reduction" of sulfates to hydrogen sulfide (H_2S), which is what sulfate-reducing bacteria do for a living. The bacteria thrive in anaerobic soil, so H_2S accumulates as the bacteria do what they do so well. Not only does H_2S smell bad, it also becomes toxic to plants in high concentrations. That led us to look for evidence of sulfide toxicity in the restored and natural marshes of San Diego Bay.

In 1987-88, John Cantilli studied the soils of the Connector and Paradise Creek Marshes to test four key hypotheses. Try not to confuse the use of H for hypothesis with the symbol H for hydrogen:

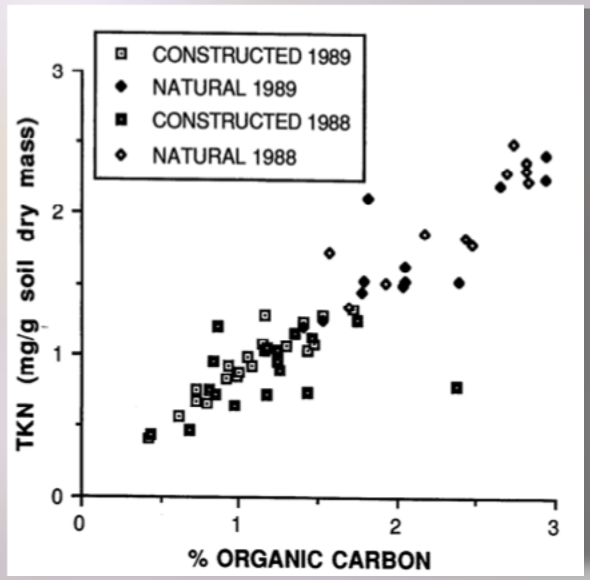
H1: Soil with greater organic matter content would have higher sulfide concentrations.
H2: Pickleweed soils would have less sulfide than those supporting cordgrass.
H3: Pickleweed would not tolerate high sulfide concentrations.
H4: Cordgrass would produce less biomass in soil with high sulfide concentrations.

John found support for most of his expectations. First (H1), soil with low levels of organic matter in the constructed marsh were likely responsible for low concentrations of sulfide. Second (H2), pickleweed occurred where the soil had lower sulfide concentrations, and third (H3), pickleweed was sensitive to sulfide when it was added to hydroponic culture (meaning grown in water). Plants thrive where their growth is not inhibited (common sense).

The fourth result (H4) was more complex. John found no correlation between sulfide and aboveground biomass in either the constructed or natural marshes, even though sulfide was more abundant in the natural marsh. One can explain this in multiple ways: Perhaps sulfides were never concentrated enough to be toxic, or perhaps cordgrass is so tolerant that its growth was never impaired, or perhaps our measure of height (TSL in 0.25-m^2 plots) did not fully assess growth. Belowground growth might have exceeded that aboveground, but as Kathy Boyer learned in 2000, it is very difficult to measure root and rhizome growth.

A general picture emerged, however, that natural marsh soil at the lowest intertidal elevation had more organic matter, more sulfide reduction, less oxygen and less pickleweed. John documented low oxygen concentrations by measuring low redox potential with an oxidation-reduction-potential (ORP) meter. And, after writing and defending his MS thesis, he emerged with an MS degree. We benefited greatly from his interest in soil chemistry, but we had to let him graduate and move on.

Dr. René Langis, an expert in water and soil chemistry, joined PERL as a postdoc to compare restored and natural soils in Paradise Creek Marsh, which was a remnant marsh that had its direct source of tidal water cut off when acres of dredge spoils were dumped alongshore (now used for industry and port facilities). The restored marsh was 4 years old at the time of his comparisons with this natural remnant.



With extensive sampling, René learned that low levels of soil organic matter were correlated with low levels of N (see graph; TKN = total Kjeldahl N, which is named for the acid-digestion process that releases ammonium, which is measurable in the lab).

It is rare for field data to show such a strong correlation; here, 90% of the variation in TKN is explained by %OM! Low soil OM and soil N were, in turn, correlated with lower levels of cordgrass shoot biomass and lower concentrations of N in cordgrass leaves. All these patterns suggested a cause → effect relationship: Poor soil → short cordgrass (Langis et al. 1991).

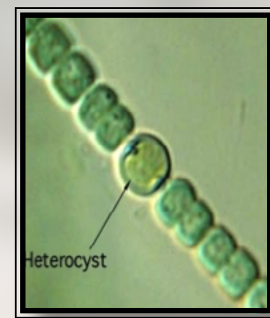
In comparison with other salt marshes, the San Diego Bay sites were generally low in soil N, although reasons for the shortage were unknown. Perhaps the diversion of streamflows cut off the supply from the watershed. At the same time that Freeway 5 was widened, the Sweetwater River was cut off by a flood control channel. As a result, most of the water from upstream was discharged straight into San Diego Bay.

René also measured N-mineralization rates (how fast organic matter breaks down) but did not find differences between the soils of the constructed and natural marshes. That meant that decomposition and release of N from organic matter was not the limiting factor. Instead, we reasoned that it must be low organic matter and low rates of nitrogen-fixation that were limiting the N cycle.

What's N-fixation?

It's something humans should know about, since we need lots of protein to grow muscles. Here's the thing: About 79% of the air we breathe is N_2 (nitrogen gas). The problem is that we (and almost all other organisms) can't use N in that form. It goes in and out of our lungs without letting us absorb it and turn it into protein. The gaseous form, N_2, is "not available."

A few kinds of organisms (N-fixing microorganisms) are able to turn N_2 into "available" compounds (containing an amine: $-NH_2$). All the rest of the biosphere, including us humans, depend on those N-fixers. Fortunately for us, there are lots of those microbes, and they are very widely distributed. Still, they need special conditions to carry out their mission in life, namely fixing nitrogen. They go "on strike" in an aerobic environment, because their key enzyme is inhibited by oxygen. Their N-fixing capability is limited to anaerobic conditions. Bluegreen algae (cyanobacteria) fix N in special thick-walled "heterocysts" that exclude oxygen.



(fine educationalmedia.pbworks.com)

N-fixers are abundant in anaerobic soils, and, when associated with roots of vascular plants, they have access to "food" in the form of organic compounds that leach out of root cells into the soil. N-fixation takes a lot of food (energy), which the vascular plants supply. In turn, the N-fixers make N available (as amines) for vascular plant growth. This is definitely a win-win relationship!

For N-fixation to occur, the salt marsh soils needs N-fixers, N_2, an organic source of energy, and moisture. With ample moisture, the soils rapidly become anaerobic, creating conditions that might support N-fixation. It is understandable that N is often limiting to plant growth in coastal wetlands. We demonstrated that fact in the Connector Marsh by adding N to sandy dredge spoils; cordgrass grew much taller where we added N than where we did not (see chapter nineteen). Note, however, that N-fixation shuts down when there is plenty of N. High concentrations of nitrate and ammonium inhibit N-fixation. Isn't that cool? It's a self-regulating process!

Malgorzata Zalejko (also called Margaret) worked with Dr. René Langis to test soils and found lower N-fixation rates in the constructed Connector Marsh than in the natural Paradise Creek Marsh. **H**er field/lab approach supported her hypothesis that the constructed marsh would have less soil organic matter, which would supply N-fixing microbes with less "food" or sources of energy in the soil (root biomass and particulate organic matter), leading to lower N-fixation rates. She also measured soil moisture in all four seasons. To avoid complications from other factors, she sampled both marshes at the same intertidal elevation and under the canopy of cordgrass.

- Roots and soil were cored with an 8-cm diameter PVC pipe beveled to make a sharp edge inserted to a depth of 10 cm and removed. In the lab, Margaret measured a proxy for N-fixation, called acetylene-reduction. The enzyme that allows N-fixers to convert N_2 to useful amines is nitrogenase, and because this same enzyme also reduces acetylene to ethylene, you can put a soil sample in an air-tight chamber, add acetylene and, up to 24 hours later, measure any reduction in acetylene using a gas chromatograph.
- Margaret sampled roots by sieving soil from 10-cm-deep cores, collecting the roots remaining on the sieve, drying them in a 75-80^{o}C oven for 48 hours and weighing them on a high-precision balance.
- She measured organic matter by drying and weighing subsamples of soil, placing the dry sample in a ceramic crucible, and burning the material in a kiln (combustion furnace). Weight loss is proportional to the dry soil's organic matter content.

As hypothesized, the natural salt marsh tended to have more moisture, more organic matter, more N-fixation and more N in the soil. It makes sense that those variables would be correlated, as each affects the other. Small-scale spatial variability and seasonal variations, however, made the patterns complex.

• N-fixation was always greater in 1-cm-deep cores, along with higher organic matter concentrations. Roots added variability to the 10-cm-deep cores after July, when cordgrass growth peaked. Before July, the natural marsh soil had more N-fixation and more organic matter in the top 10-cm; after July, the constructed marsh had more N-fixation and more root biomass. In September, it is possible that high soil N inhibited N-fixation in the natural marsh.

• It was a lot of work collecting all those data in the field and then measuring N transformations in the lab! For her heroic efforts, Zalejko received her MS degree and was a co-author on three papers that revealed secrets of soil nitrogen in San Diego Bay's restored salt marshes.

A functional equivalency index

Functional Equivalence	**57%**
Soil organic matter	51%
Sediment inorganic N	45%
Sediment total N	52%
Soil water inorganic N	17%
N-fixation in soil (0-1 cm)	51%
Rhizosphere N-fixation	110%
Plant biomass	42%
Leaf N concentration	84%
Canopy height	65%
Epibenthic inverts density	36%
Epibenthic invert species lists	78%

On the left is our comparison of soil attributes (in the constructed marsh as a proportion of the same attributes in the natural marsh), including the sil invertebrates, discussed next. We estimated that constructed-marsh functions were ~57% of those in the natural marsh (Zedler and Langis 1991). For two sites to be functionally equivalent, the average would be closer to 100%.

Overall, the natural and constructed marshes functioned differently, and nitrogen was limiting.

Nitrogen dynamics include N-fixation by cyanobacteria, accumulation of N-rich organic matter, N uptake by vascular plants, decomposition and N mineralization. It might take years for the constructed marsh soil to become equivalent to natural marsh function, given the slow accumulation of soil organic matter in restored marshes.

• If you like mud, here's a suitable career for you—studying soils in restored wetlands. Soils take longer to restore than many of the salt marsh plants and animals. Some aspects of soil, notably their organic matter (OM) content, could take centuries to match natural salt marsh soils.

• Climate might be a limiting factor in southern California. The year-round warm climate likely speeds up the decomposition of OM. Bacteria and fungi (decomposers) are temperature-sensitive. Warm them a bit, and their metabolism speeds up. They burn more OM, so there's less to accumulate as soil OM.

Does tall cordgrass depend on soil or genetics?

Ecologists around the world have wondered for decades why cordgrass is sometimes really tall and robust and sometimes wimpy. Some said the genetics controlled these differences; others said it was the different environmental conditions where they were growing. Debates led to many papers and convincing talks at scientific conferences.

Then, in 1995, Dr. Denise Seliskar (U. Delaware-Lewes) published a convincing study. She and Dr. Jack Gallagher reared three morphologically distinct genotypes of the Atlantic Coast's smooth cordgrass (*Spartina alterni lora*). The parent plants came from Massachusetts, Delaware (DE), and Georgia. After 11 years of growth in a "common garden" Denise and Jack dug up and planted the offspring of the three genotypes into a large restoration site in DE. Each genotype had its own plots in the intertidal restoration site. The next part was easy; they waited and watched several ecosystem functions diverge (change in relation to the genotype). The functions were productivity, decomposition rates, and animal uses. Each genotype produced stands of cordgrass that had unique structure (appearance), and all three functioned differently. Their work was a compelling demonstration of cause → effect. Genetic differences can cause functional differences. But are genetics always responsible for tall cordgrass?

Wow!

The DE study was relevant to our restoration projects, because wetland managers wanted our native cordgrass to grow tall to support rail nesting. Should restorationists plant propagules from tall parents or should they just provide environmental conditions to grow tall canopies? Or maybe both. Read on…..

Sally Trnka rose to the challenge of testing "nature versus nurture." She was the first to evaluate parental effects in our native cordgrass, although we knew of many places where plants were taller (near channels and bay edges) and when they grew taller (after river flooding, salinity dilution, and nitrogen addition).

Sally's "common garden" was a newly graded channel edge in Mission Bay. The sandy substrate was low in nutrients and high in salinity, but the elevation range matched that in the adjacent natural cordgrass. Next: Some fun in the sun (and mud). She collected tall and short cordgrass ramets from nearby Rose Creek and San Diego River--which were already disturbed. We did not rob the remnant natural marsh! Short ramets averaged 65-70 cm, and tall ramets averaged 102-112 cm.

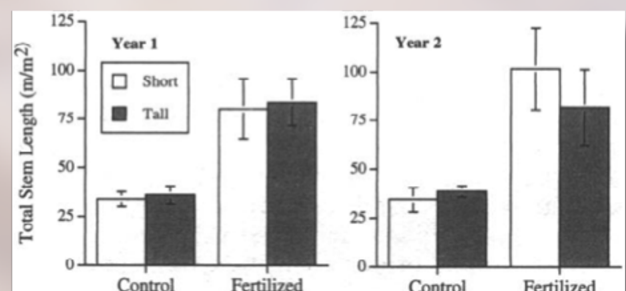
More fun in the mud: Sally planted four experimental blocks, each with ramets from Rose Creek and San Diego River, each with both parental heights (8 tall ramets and 8 short). Then it was the plants' turn to work, that is, to photosynthesize, grow and form new clones. After a year, Sally measured stem number, maximum height, the number of flowering stems, and patch diameter. And, of course, she measured soil variables: texture (sand, silt, clay), salinity, organic matter, and nitrogen.

For added scientific rigor, Sally set up an experiment at the outdoor PERL site. Using 36 small tubs (56-cm diameter) and tall and short ramets from four collecting sites (same as above plus two from Tijuana Estuary), she tested for effects of collecting site, initial height, and a new factor, nitrogen addition. Can you guess the outcome? Did we support the importance of genetics, as in the DE study, or were environmental conditions more important in southern CA?

We found support for both "Nature and nurture." In support of Nature, parental height had some effect on offspring that grew in Mission Bay. But the results were complicated—for San Diego River plants, short parents produced taller plants than tall parents, while Rose Creek plants performed more understandably: tall parents produced taller offspring than short parents. Hmmm; it was a weak effect but a confusing result. More research….

In support of Nurture, we found much stronger results (greater differences) where we controlled environmental conditions using mesocosms. Sally provided low-salinity, sandy loam soil, and compared growth with and without nitrogen additions.

Cordgrass in mesocosms (Trnka and Zedler 2000).



In Mission Bay, parental height did not determine cordgrass height of offspring in the restoration site with poor (sandy and low-nutrient) substrate, but plant growth did differ with the exact position where we planted them (blocks), which indicated that local environment influenced growth.

In mesocosms, adding nitrogen increased maximum height (104 cm versus 90 cm) and really increased the number of stems, so that total stem length more than doubled (TSL= 82 versus 35 meters per m2). The difference in TSL persisted into year 2 because of continued high density, but not taller stems.

As described in the preface to this e-book, the structure and functioning of California salt marshes can't simply be extrapolated from (based on) science done in salt marshes along the Atlantic Coast. The DE study provided a hypothesis for cordgrass collected from MA, DE and GA, but ramets from southern California did not offer support for strong genetic signals. That makes sense, because the genotypes tested in DE were from very distant locations, and they were probably far more different genetically than the ramets Sally collected within San Diego County. Still, the Sally's finding is significant. It means that cordgrass growers in San Diego County do not have to rob tall plants from our finest remnant marshes; instead, they can collect seeds and grow ramets in nitrogen-enriched soil to achieve tall canopies.

What about marsh invertebrates and their foods?

We knew that salt marsh epibenthic (on the substrate) invertebrates feed on detritus. We did not know whether their populations or their food supplies in restored marshes were as abundant as in natural marshes. Sue Rutherford (later Sue Scatolini) volunteered to find out. That was shortly after she had won an international body-surfing contest. I was impressed, even though I wasn't quite sure what body-surfing entailed. If she could beat global contenders, she could master invertebrates!

Sue hypothesized that:

H1: Litter would decompose faster in the natural marsh than the constructed marsh.
H2: Litter would decompose faster with more species and more individuals of epifauna.
H3: Epibenthic invertebrates would be more abundant where soils were wetter (lower elevations) and where cordgrass was more dense, including a seasonal pattern with increasing biomass.

We developed a new sampling method by sewing litter bag traps (30x30 cm) and filling them with cordgrass stems and leaves. The bags served two purposes: measuring the rate of biomass decomposition (weight loss over time = detritus production) and trapping invertebrates. By using some bags with 2-mm mesh and others with 4-mm mesh, we separated the effects of larger animals (which could not enter the 2-mm-mesh bags) from those of the smaller epifauna. Additional bags were filled with cattail, bulrush, or plastic shreds to evaluate the utility of cordgrass as "bait." Indeed, litter bags filled with cordgrass were the most effective traps for epifauna.

In all, Sue trapped 45 species of epifauna and 43,531 individuals in her many litterbags. Of those, a whopping 17,711 (41%) were fly larvae! The larvae of flies and a few other insects were terrestrial species that used the marsh surface. A slightly larger number were marine organisms--polychaetes and crustaceans. Some 10% were molluscs. The abundant species were, in decreasing order: a fly larva (*Pericoma* sp.), a polychaete (Capitellid) worm, the rock louse (*Ligia occidentalis*), the beach hopper (sand flea, *Orchestia traskiana*), biting midges (*Culicoides* species) and the shore crab.

Rock louse (www.wallawalla.edu)

Beach hopper (academic.evergreen.edu)

Shore crab (archives.evergreen.edu)

Sue rejected H1 when she found that cordgrass litter decomposed at the same rate (93-98% loss per 8 months) in the natural and constructed marshes (age 4 years). However, the constructed marsh did not match the natural reference marsh in all attributes.

A single litterbag trapped from 6 to 1392 invertebrates, with a mean of 260 per bag. Counting all those animals under a dissecting microscope required a champion, such as one with surfing prowess! Sue trapped similar numbers of species in both marshes (34 species in constructed; 37 in natural), but the differences in numbers were among the uncommon species, not the 7 most abundant.

The natural marsh supported 2-3 times as many invertebrate individuals as the 4-yr-old constructed marsh. However, the constructed marsh supported many more young yellow shore crabs (*Hemigrapsus oregonensis*). Low numbers of invertebrates could limit food available to marsh carnivores. H2 was rejected because decomposition rates and invertebrate species richness were similar in the restored and natural marshes, despite differences in invertebrate abundances. Decomposition rates in litter bags were not different due to numbers of species or invertebrate abundance.

Instead, the data suggested environmental effects. H3 was supported by Sue's data. She trapped more invertebrates in lower than higher elevations and more in fall than in winter. In the natural marsh, she found twice as many invertebrates in litter bags placed under ~80% cover of cordgrass compared to places with <20% cordgrass cover. Here's a question for further research—were fewer invertebrates produced in open areas, or were the same numbers produced and more removed by predators? The litter bag traps could not measure predation.

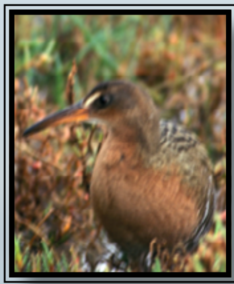
Sue's study revealed another secret that was hiding in the constructed marsh, namely, the presence of an exotic mussel (*Musculista senhousia)*. This mussel is an opportunistic invader that grows and reproduces rapidly, covering other species that might otherwise occupy benthic substrates. Years later, that species became the focus of Jeff Crooks' dissertation research at Scripps Institution of Oceanography.

Attempts to restore rail nesting habitat in Sweetwater Marsh

In chapter three, I described the basic needs of the light-footed clapper rail. Some of those secret needs were uncovered when CalTrans tried to restore its nesting habitat in San Diego Bay's Sweetwater Marsh. Where the rails *wouldn't* nest provided the clues.


Osprey (NASA photo)

Clapper rails are so well adapted to the lower intertidal zone where cordgrass lives, that it seems they could teach a course in hydrology. Is this a bird or a hydrological engineer? Where is the water deep enough to discourage terrestrial predators, like coyotes and reptiles, yet shallow enough to allow nest construction that can protect them from predators that fly over the marshes, like osprey and harriers?

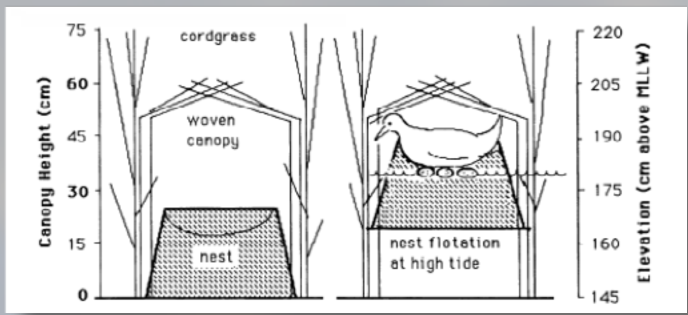


Avoidance of threats is a good strategy—birds in search of nest sites just need to find the optimal elevation and optimal time of year to avoid the highest tides (see nest model below). Then, they need to build a nest in tall camouflaging vegetation (dense cover), and anchor the nest so it won't wash away in a storm.

HOW TO FIGURE OUT WHAT A CLAPPER RAIL NEEDS: We knew tide heights from tide tables, rail nest thickness from Paul Jorgensen's work, nest elevations from Richard Zembal's work at Upper Newport Bay, growth rates of cordgrass in natural marshes, and the heights of plants in restored marshes. The next step was to predict just how tall stems of cordgrass would have to be in March to allow birds to construct nests and to be safe from flooding and aerial predators.

A clue was the big difference in cordgrass heights between natural and restored marshes. By comparing heights of cordgrass in marshes where rails did and didn't nest, I established criteria for "suitable habitat," namely, at least 100 stems/m^2 with at least 90 stems/m^2 >60 cm, of which at least 30 stems/m^2 >90 cm in height. This was my analysis:

Birds nest between March and July, and their nests are built at 145 cm MLLW on average. So, my model nest is at ~145 cm and about 20 cm thick so that the nest rim is at ~165-170 cm MLLW. At low tide on the left, the nest is dry. But such a nest is not high enough to avoid extreme high tides during nesting season. The rails seem to know that, because they make their nests out of dead cordgrass stems, which are hollow. Voila! The nest can float (on right).



Nest model (Zedler 1993)

Rails also attach their nests to vertical stems so it won't float away during wind storms or water surges. Finally, they weave a canopy overhead like a gazebo to hide from raptors and hold the nest in place in case an extreme tide makes it float too high. At high tide, and with 20 cm of flotation, a 75-cm-tall cordgrass canopy would be tall enough for a woven canopy to hide the nest. And if 75 cm is the midpoint of a 60-90 cm tall canopy, then that range should attract birds to nest, whether stems are live or dead.

March is when high tides aren't very high (chapter two). The tidal amplitude is minimal during egg laying, and it increases toward the end of brooding and chick hatching. The birds really need tall plants during their 21-day gestation period, plus the next few weeks while the chicks are maturing. These are the most vulnerable times of the bird's life. I'm sure it's no accident that clapper rails begin nesting in March. Rails that nest earlier would be vulnerable to higher tides and winter storms; birds that nest later would be vulnerable to high tides in May and June. Natural selection would eliminate non-adaptive genetically-controlled nesting behavior.

At Sweetwater Marsh, the US FWS required the CalTrans to provide home ranges for seven nesting pairs of clapper rails in exchange for damaging part of Paradise Creek Marsh during the widening of Freeway 5 in Chula Vista (see chapter three). Information from Dick Zembal and Paul Jorgensen indicated how much area was needed for each pair of rails (~2.5 acres). CalTrans graded eight intertidal islands to just the right elevations and planted cordgrass from healthy "plugs" (vegetative units grown in pots). The grass grew, somewhat, but the rails did not come. They were right next door in the natural marsh remnant, but they did not nest in the Connector Marsh. How would you decide if the home ranges met the requirements of FWS?

Each home range had to meet all eight criteria: Each home range must have high marsh, low marsh, and mid marsh habitat. We needed sampling methods that we could repeat year after year, while waiting for all seven areas to meet all eight criteria. Where should we look for potential nesting habitat? We joined forces with remote sensing experts and came up with the following approach.

Dr. Doug Stow from SDSU's Geography Department is an expert in using remote sensing methods to distinguish vegetation.

Doug brought Stuart Phinn on board. Stuart was a PhD student who wanted to learn remote sensing techniques while solving the challenge to find potential nesting sites.

The trick was to obtain low-elevation photos with high resolution of light reflection. Stuart and Doug used a multi-spectral camera that was new technology at the time. Other people had used four bands of reflected light to calculate an index called NDVI (Normalized Difference Vegetation Index), but we needed greater detail. Stuart applied image classification techniques to high-spatial-resolution digital video imagery (0.8-m pixels) to delimit patches of different marsh vegetation (Phinn et al. 1996, 1999).

The multi-spectral imagery led to maps of cordgrass and marsh-plain succulents and high marsh subshrubs, and suggestions for potential 2.5-acre home ranges for clapper rails. Then Stuart estimated the area of each vegetation type in each home range. In the above map, you can see tiny green patches with >90% cover of vegetation that might have tall cordgrass. The larger yellow polygons (cover estimate <90%) could make up part of a home range.

High-resolution mapping from low-elevation multi-spectral imagery was a leap forward for monitoring salt marsh restoration in southern California. Using the above map, we outlined seven 2.5-acre potential home ranges and ground-truthed (checked on foot) the vegetation to see which might meet the eight criteria. The pie chart on the right shows the three types of habitat that were required: high marsh (2 green wedges), low marsh (4 blue wedges), and mid marsh habitat (2 reddish wedges). For example, at least 15% of the home range had to be dominated by cordgrass and at least 100 m^2 of cordgrass had to be *dense* (≥90% cover) and *tall* (≥60 cm).

Our 1997 data for each of the 7 potential home ranges are on the right. Black wedges indicate criteria that were not met during many years of restoration. Which one met all the criteria? Answer: The fifth pie has no black wedge. Which wedge was usually black and which criterion does it represent? Answer: It's the tall cordgrass that was most often not found.

These sites were supposed to support rail nesting, but at age 8 years (3 pies on left) and 13 years (4 pies on right), they were not attracting rails to nest. With only 1 of 7 potential home ranges meeting all 8 criteria, including tall cordgrass, we concluded that the birds wouldn't nest in the restored marshes because the cordgrass was too short. FWS agreed, and we ceased monitoring in 1997.

Read further to see why we concluded that cordgrass would never grow tall enough at this restoration site. When we returned to the site in 2014, cordgrass had less cover than in1997, and rails had still not nested. Our 1997 conclusion was correct.

You might wonder what the Connector Marsh connects? It links the north and south islands after the US Army Corps of Engineers (ACE) built a flood control channel that separated them. Part of idea was to allow courting rails to find one another. Because the flood control channel dissected habitat for an endangered bird, ACE left gaps in the channel levees. So, the excavated channels linked Paradise Creek Marsh to Sweetwater Marsh and allowed rails to "connect" with one another. Any rails to the north might then be able to hear mating calls from down south and have a "line of sight" to find a mate.

Sweetwater Marsh; with constructed marshes outlined in blue & green

This was quite an attempt at matchmaking! Finding out whether or not it worked would have required a lot of watching for birds or cameras to record movements, neither of which was required by FWS.

Why was cordgrass so short in restored marshes?

Like much of science, one answer led to another question. In this case, *why* was the cordgrass too short for rail nests in restored marshes? Assuming we could figure that out, the next question would be: Can we eliminate the factor that limits cordgrass growth and create marshes that *will* sustain (maintain long term) tall cordgrass and support clapper rail nesting?

As Sally Trnka's work showed, the likely causes were not genetic but environmental. The soil was missing critical nutrients that help plants grow tall. With lots of ideas from the studies discussed above and the salt marsh literature, we decided to focus on nitrogen, commonly known to limit plant productivity in coastal wetlands. We had already shown that the soils of restored cordgrass marshes had lower N content. Next, Kathy Boyer added nitrogen in controlled field experiments to see if cordgrass would grow taller. When it was clear that the restored marshes needed more N to support tall cordgrass, we set up a long-term experiment to determine when we could stop adding N: When would cordgrass become self-sustaining (persistent without human help)—which was one of FWS's requirements.

For five years, we added N, and each year we tested to see if the soil could hold enough N to sustain tall cordgrass (Lindig-Cisneros et al. 2003). We knew that a year was not enough. After two years, three years, and four years, there was still not enough N in the soil for cordgrass to grow tall the next year. After five years, we called it quits. A need to add N for five years could not be considered "self-sustaining" tall cordgrass. We predicted that tall cordgrass would never be self-sustaining. The project ended with agreement (by US FWS, US ACE, and CalTrans) that the site could not provide suitable nesting habitat, so efforts to do so were aborted, and PERL ended the monitoring and assessment program.

What else can limit restorability?

SEED: Will supply meet demand? A few years ago, a paper in the journal *Science* asked: "How are large-scale (100- to1000-km^2) plant reintroductions that recreate biodiverse communities to be achieved?" The authors (Merrit and Dixon 2011) were concerned that efforts to select and store seeds (creating artificial seed banks) would not meet demands if the areas needing restoration could actually undergo restoration. They called current efforts "stamp-collections" when future needs might total a metric ton of seeds per species. They argued for seed banking to progress beyond collecting and storing seeds to farming seed, training the work force, and educating the public.

The southern California coast has several large restoration programs and no central seed bank. Which species should be introduced once sites are constructed and where should seeds and ramets come from? I don't think we know enough about the genetics of either the source populations or the recipient marshes.

The precautionary principle applies, namely: when we don't know enough, our actions should be conservative, rather than daring. Using nearby sources of seeds and ramets would be conservative; widely separated donor sites would be daring.

WILL A TON OF SEEDS BE NEEDED FOR EVERY SPECIES? I question the concept that all species need to be reintroduced using large amounts of seeds. A conservative approach is to begin restoration with a matrix dominant (Frieswyk et al. 2008)—one that can co-exist with other species rather than displace them. Perennial pickleweed is often a monotype dominant, and it crowd out its competitors. Also, it doesn't need to be sown or planted. It readily invaded the 20-ac Model Marsh without help!

Salt marsh daisy and alkali heath (on right) would be suitable matrix dominants to establish widely on newly graded marsh plains. Both persisted as subordinates with perennial pickleweed at the Tidal Linkage. Smaller numbers of seeds of other species could be added in "diversity hotspots." This could also be done later, in places where people from the local community might want to plant and track outcomes of seed-sowing efforts. Once established in patches, such species could spread on their own where conditions become favorable. I recommend mapping using GPS units, rather than marking sites with stakes or flagging. Interested volunteers could track the expansion of other species.

Adding heterogeneous topography (chapter eight) would also reduce the numbers of seeds to sow. As described earlier, annual pickleweed can co-exist with perennial pickleweed where there are shallow pools and an initial seed source. Once established in a few places, this annual could produce hundreds of seeds per patch, reducing the need to sow tons of seeds.

Finally, instead of broadcasting diverse seed mixes, it would make sense to sow seeds where plants are most likely to establish. This would reduce the demand for seed. Sea blite seems to like channel edges, so that suggests specific sites for a species that would benefit from seed addition. Salt wort tolerates shallow water, so shallow depressions would be suitable sites for sowing its seeds.

WILL LARGE QUANTITIES OF SEED BE NEEDED? Restoration projects will need seeds, that's certain. In addition to restoration sites, there will also be places where salt marsh managers might want to "assist migration." Assisted migration is the deliberate planting of species beyond their current boundary. For example, as sea level rises and native vegetation becomes increasingly flooded by higher sea levels, species can be assisted in moving upslope, if they are not doing so on their own.

Clonal species should migrate more readily than non-clonal species. Those that produce runners (salt marsh daisy, salt wort) should be able to "creep" upslope as the marsh plain becomes too wet and the high marsh becomes more moist. Perennial pickleweed also reproduces vegetatively, but its rhizomes don't extend away from the parent as far as those of salt marsh daisy and salt wort. On the right, salt wort (yellowgreen runners and leaves) is crawling onto a bare spot, while perennial pickleweed (upper right) is being left in the dust, so to speak.

Plants that reproduce mainly from seed have to do more than produce seeds; they also need to disperse seeds and establish seedlings. Research from tidal marshes along the Napa River suggests that the numbers of seeds are not what is preventing new restoration sites from becoming fully vegetated (100% cover). Fewer species make up the "seed rain" than were present in the reference marsh. As a result, restored marshes had fewer species than their reference site (Diggory and Parker 2011). Not surprisingly, perennial pickleweed and bulrush (*Bolboschoenus maritimus*) were both rapid colonizers, with abundant seeds in the seed rain. Cordgrass was also a rapid colonizer, but less widespread in the restoration sites. Salt wort became a co-dominant, but four species were missing, not only in the new marshes but also in the seed traps, which indicates they are not good dispersers. They were: *Artemisia douglasiana, Frankenia salina, Glaux maritima*, and *Lathyrus jepsonii* ssp. *jepsonii*.

In Tijuana Estuary, Roberto Lindig-Cisneros found that only 3 of 8 marsh-plain halophytes spread readily at the Tidal Linkage restoration site, even though seedlings were planted in nearby plots within the same site. Of those 5, seed supplies might become limiting for annual pickleweed and sea blite (the 2 short-lived species). They might become limited to shallow pools and creekside habitat, as described earlier.

The most likely self-colonizer is perennial pickleweed. Its floating seeds disperse widely, and its seedlings establish readily during winter-spring (as you can read about shortly). Given rapid sea level rise, some areas might need planting, for example, where inundation occurs faster than this species can move upslope. Still, a preference for locally-adapted plants suggests that we should not set up a central seed bank for the region. Instead local nurseries could provide native plants from known sources to meet future demand for seeds.

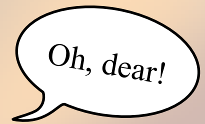
Above: Model Marsh in year 3, with cordgrass plantings south of the bare mudflat.

Below: Model Marsh in year 4, with perennial pickleweed colonizing the mudflat;
Brown cordgrass is behind the green pickleweed in this photo.

There was no need to plant perennial pickleweed. Within five years, the Model Marsh was a near monotype (single-species stand) of perennial pickleweed. How did that happen?

Hem Morzaria-Luna installed a floating net trap on the large tidal channel that flowed into the Model Marsh. The trap was designed to capture seeds that would float into the site. By setting up seed traps during each season, she learned that tides disperse seeds during high spring tides and mainly in winter, after fruiting of perennial pickleweed. Rather than counting every seed and trying to identify it to species, she placed captured seeds on soil and counted emerging seedings.

Of 37,675 seedlings from seeds trapped in the Model Marsh, over 99% were perennial pickleweed (Morzaria-Luna and Zedler 2007). There is no need to plant this species where a nearby marsh can supply seeds! Tidal marsh restoration largely depends on natural seed rain to revegetate restored sites, but we don't know enough about the abundance and composition of seed inputs or the limitations of individual species' dispersal or recruitment abilities.



Along the Napa River, northeast of San Francisco Bay, three marshes that were restored to tidal flushing had fewer species than one reference tidal marsh, as mentioned earlier. Species that were missing in the restored sites were also missing in the seed input, suggesting dispersal limitation. Although many seeds were washed away, the remaining seed seemed adequate to revegetate bare sites, even if some species were missing. Species with high seed production were good at colonizing bare sites, and they produced more seeds on site. That kind of positive feedback is a key to self sustainability. Many seeds à establishment à more seeds.

Two confounding variables might have influenced the outcomes along the Napa River, since the reference site was less inundated and more saline in summer. It is extremely difficult to find places in nature that are identical except in the one variable you want to assess. That's why ecologists like to set up controlled experiments.

But as you know by now, controlled experiments have other shortcomings. Weeding, for example, is useful in testing hypotheses about species interactions, but weeding is not a natural phenomenon. We showed positive correlations between species-rich plantings while plots were weeded, but not after weeding ceased (Doherty et al. 2011).

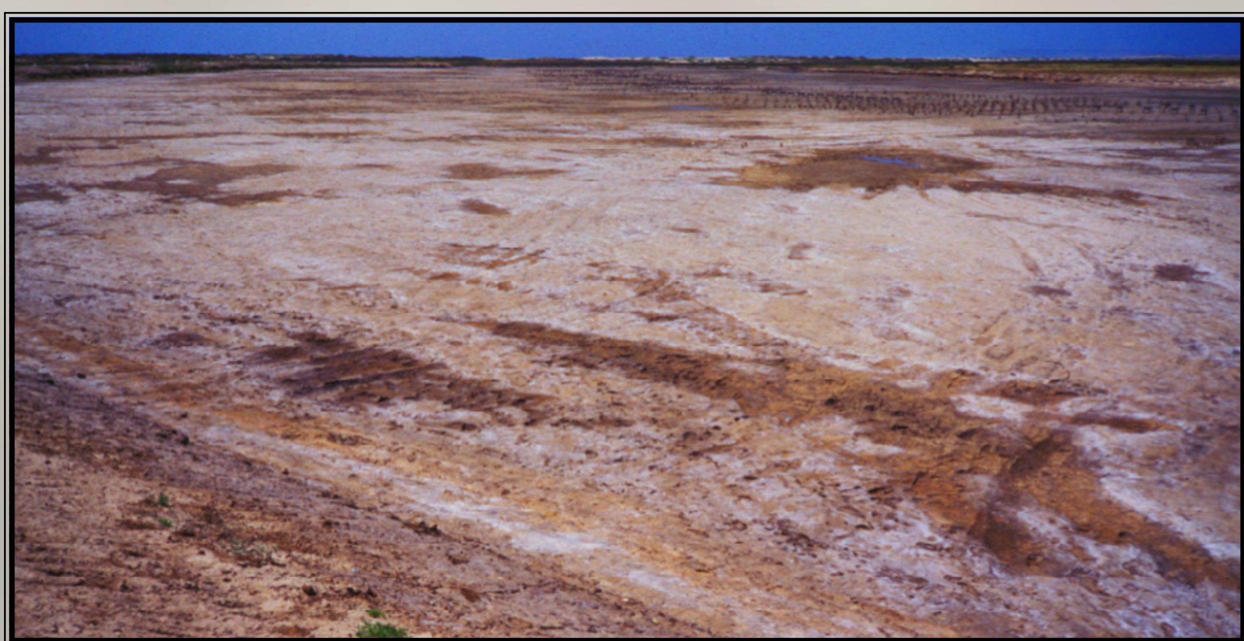
PLANTING SEEDLINGS.

Erin O'Brien tested alternatives for planting greenhouse-grown seedlings by comparing tight (10 cm apart, see photo on right) and loose clusters (90 cm apart) on the Model Marsh plain. She found that tight clusters increased survivorship by 18% compared to loose clusters.

The advantage of being planted in a cluster might be that a group of plants reduces wind or waves. But because the differences in survival were small, it would be helpful to have more tests of clusters, with a greater variety of spacings. Erin also found that being near a tidal creek network increased survivorship of salt wort and salt marsh daisy by 20%. Growth rates of survivors were similar, however (O'Brien and Zedler 2006).

WHY SO FEW SEEDLINGS IN OUR MODEL MARSH EXPERIMENT? Believe me, it wasn't our intent! We were limited by low numbers of seedlings left in our greenhouse after our first experimental planting of >5,000 seedlings failed (nearly all died). You can see what happened below. What a catastrophe! There was a delay in the opening the marsh to tidal flushing. Instead of being opened to receive the winter high tides, the marsh plain dried out and became a hypersaline salt flat (Zedler et al. 2003). The site did become tidal until 14 Feb. 2000, and tides weren't high enough to leach out salt, as you can see below.

We had to regroup and reassess our resources and design new experiments. We felt fortunate to have enough seedlings to test cluster spacing and distance from tidal creeks—but we waited to plant them until the marsh plain was wetter and less saline, following high tides.



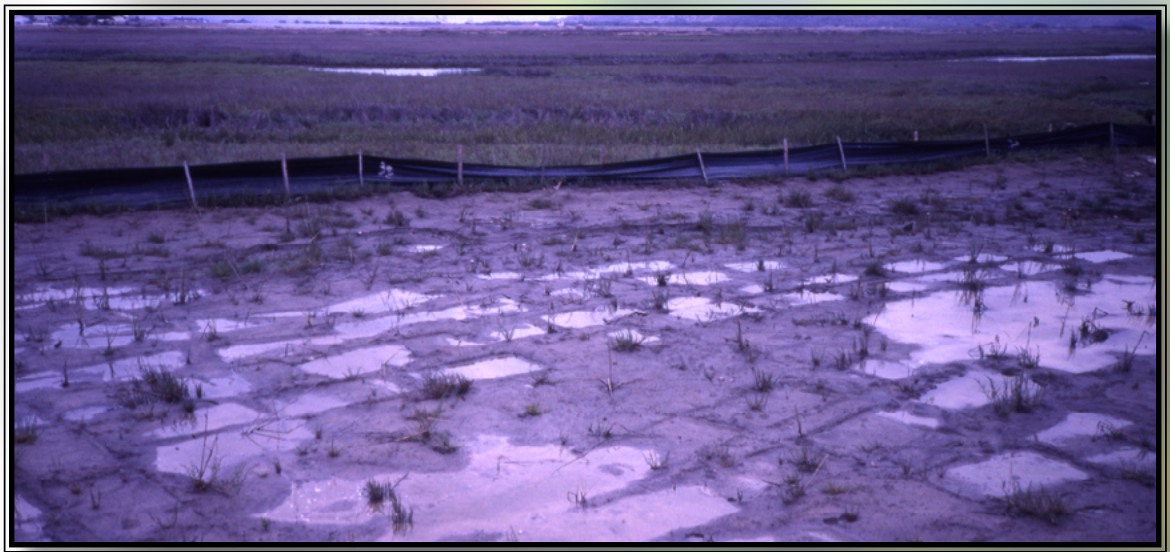
Can you see any of the 5,000+ seedlings that we planted? Neither can I! The plugs of cordgrass in the upper right are the only signs of life. This photo is from April 29, 2000.

In Huntington Beach, seedlings were planted 20 cm apart and watered twice daily with a freshwater sprinkler system. All had high survival (Blair et al. 2013). All plots were 2x2 m, each planted with 81 seedlings, along a high-marsh berm at Brookhurst Marsh. Restorationists compared monocultures of perennial pickleweed with a polyculture of the pickleweed plus 8 common species (glasswort, saltwort, alkali weed [*Cressa truxillensis*], saltgrass, alkali heath, goldenbush [*Isocoma menziesii*], salt marsh daisy [a.k.a. salty susan], and love grass [a.k.a. shoregrass]).

Both planting treatments achieved 100% cover within a year. The polycultures had more complex canopies (also found by Georgeann Keer at the Tidal Linkage). Species with trailing stems (salt marsh daisy and salt wort) spread beyond their planted plots faster than perennial pickleweed. Macrofauna were similar within the two planting treatments. Over time, however, plant cover increased and so did the number of species and abundances of mobile ground-dwelling fauna (caught in pitfall traps), benthic infauna (captured in soil cores), and canopy insects (sampled by converting a leaf blower into an "insect sucker").

Larger test plots might allow researchers to show differences among mobile animals. Small plots always risk error or bias in deciding which species is in the plot. More information on mono- versus polycultures would help understand effects on animals. Could the animals fly, walk or slither from plot to plot? Might invertebrates respond to the mosaic of plots, regardless of single or multiple species in small plots? Was twice-daily irrigation needed? Because of recent droughts, some irrigation was probably essential. Does the short (18-month) study make it risky to extrapolate to other restoration projects and longer-term outcomes? Despite my questions, which just indicate interest, this study was unusually ambitious in assessing plants, algae, invertebrates and stable isotopes. You can find Blair's MS thesis online.

PLANTING PLUGS. For plants that do not grow dependably from seed, growers often put small plants in greenhouse pots or large beds to propagate (increase their numbers) them vegetatively. When a restoration site is ready, they dig up ramets and attached soil. The resulting plugs are commonly used for planting cordgrass. Can you think of a disadvantage of this method? Hint: Will the ramets be genetically diverse? No, the new ramets will be genetically identical to the parents. Plantings from seed will be much more diverse. Growers should start with seeds from multiple plants, so the seedlings are diverse. Diverse seedlings could be propagated vegetatively.



Seacoast Drive restoration at Tijuana Estuary planted by Chris Nordby—nice work.

SHOULD CORDGRASS BE INTRODUCED TO A SALT MARSH WHERE THERE'S NO HISTORICAL RECORD OF ITS PRESENCE? I think so, as argued earlier. If tidal influence is being restored, then the tidal marsh is an appropriate restoration target, and cordgrass is a component of that ecosystem. It is unfortunate that historical records are short-term and incomplete and that we don't really know where each species occurred historically. Cordgrass is a grass, and grass pollen grains that are used by paleoecologists (researchers who identify species present in deep sediment cores) are pretty similar. So we might think that cordgrass was absent when it was actually present a long time ago. How far back should we look for hints about historical marsh composition? No clear guidance comes to mind. Sometimes, we just have to use our best judgment. I think it's more important to retain all the native species somewhere in the southern California biogeographic region than to replace them exactly where they were found in recent records. Still, I respect others who think differently, since we never know for sure how re-introducing a different set of species will affect the others.

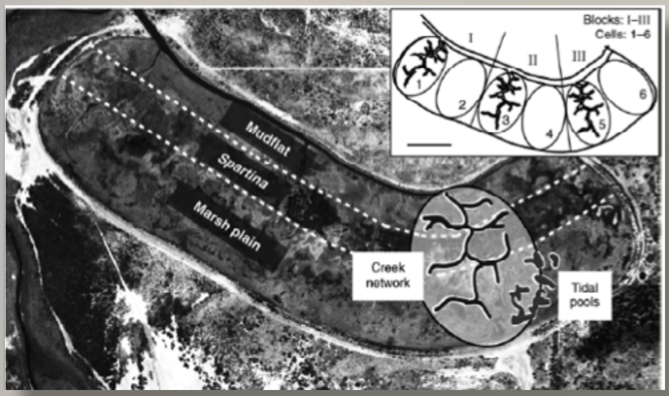
What about restoring the animals?

While "nesting sites" are often added to wetlands to protect birds from terrestrial predators, the common assumption is that most birds and other animals will "self-restore" once the vegetation and soils and hydrology are restored. Various observations support this assumption.

When Tijuana Estuary closed to tidal flushing for 8 months in 1984, the invertebrate and fish fauna and clapper rails met their demise. Recovery began as soon as the river-ocean mouth was breached by bulldozers, however. The hypersaline water was replaced by seawater with its many organisms, ready to colonize the substrates that were rewetted and leached of excessive salt. Over about four years, the clapper rail population recovered.

At the newly excavated Model Marsh, shorebirds gave us the first clue that the infauna were recovering. They came in flocks to feed on the bare marsh plain—which was actually more mudflat than marsh for the first 2 years. As the pickleweed colonized and vegetated the marsh plain, shorebirds were no longer interested, because they prefer to feed in open areas. Larkin's summary of our study of the marsh and creek invertebrates and fishes showed that naturally occurring assemblages were developing without any help from humans.

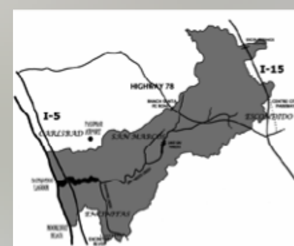
Between years 2-3, perennial pickleweed became dominant, and after extreme sedimentation in 2004, plant cover increased from 12% to 53% on the mudflat, 76% to 97% in the cordgrass, and 8% to 21% on the marsh plain (based on aerial photos). After 6 years, 42% of the marsh plain remained as pools (data of A. Varty). The pools were hotspots for invertebrates and feeding oases for killifish (Larkin et al. 2008).



Salt marsh animals that are short-lived and have many offspring seem pre-adapted for self-restoration. Still, some species were lost when Tijuana Estuary was subjected to freshwater flooding in 1978 after many decades without freshwater flooding. Large and diverse infauna were abundant (reported in Zedler et al. 1992). After 1978, the estuary was jolted by frequent floods and sedimentation, and the channel fauna shifted toward short-lived species that had greater resilience, meaning ability to bounce back. The "shifting" was caused by sudden changes in the salinity and other variables. Flooding would have killed millions of stationary animals, while making room for new recruits to colonize fresh sediments and replace the previous residents.

Estuaries are dynamic places! How might the impacts of natural flooding differ from the impacts of human-caused disruptions, such as road building through an estuary?

Recent restoration projects



www.batiquitosfoundation.org

Batiquitos Lagoon was restored to full-tidal flushing to compensate for impacts of dredging San Pedro harbor and adding port facilities for Los Angeles. Decision-makers agreed that restoring tidal flushing to an ~80-acre nontidal lagoon in Carlsbad would compensate for destroying coastal habitat in Los Angeles.

The lagoon had reduced tidal flows following construction of the California Southern Railroad (1881), Pacific Coast Highway (1912), and Interstate 5 (1965). Talk about cumulative impacts! The outcome of all that filling was a mouth that remained blocked for ~90 years. Then, with agriculture and urban development, the water quality degraded, algal blooms led to fish kills, and resource agencies wanted restoration.

The 2.5-year dredging project ended in 1997, when the site was opened to tidal influence. The lagoon is now a Marine Protected Area and a Nature Reserve of the CA Department of Fish and Wildlife.

Bolsa Chica Lowlands (right) is southern California's largest restoration project. Tidal flushing was returned to >600 acres after over a century of nontidal conditions. Restoration involved removing and repairing areas used to extract oil, excavating a new tidal embayment and ocean inlet, constructing a new highway bridge, and establishing aquatic and intertidal vegetation, while preserving some wetlands.

(www.bolsachicarestoration.org/project.php)

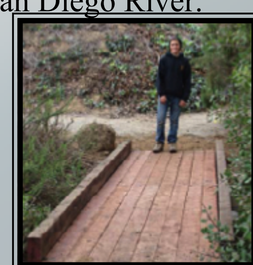
The project site was opened to tidal flows on 12 August 2006. Endangered birds (western snowy plover and California least tern) are using the nesting sites that were designed for their use (20 acres total for the Full Tidal Basin, Muted Tidal Basin, and existing Seasonal Pond).

San Diego Bay salt pond restoration is underway, with the return of tidal flows to 220 acres in the southwest corner of the bay in 2011, after 50 years of being nontidal (www.fws.gov). Restoration required involved a floating dredge recontoured the site and created the tidal creeks that you can see in the photo. Next, levees between the two ponds were breached so the bay waters could flow in and out with the tides.

Restorationists planted >40,000 ramets of cordgrass plus thousands of middle and upper marsh plants. A new and diverse array of organisms began to thrive in the new tidal ecosystem. Birds were quick to notice and take advantage!

Famosa Slough is an isolated fragment of the Mission Bay-San Diego River system. It benefits from its unnatural isolation--tucked away from the jet skis and motor boats in Mission Bay and protected from sediment and nutrients that flow downstream from the San Diego River.

The local Friends of Famosa Slough helped the City of San Diego establish the Famosa Slough Wetland Preserve, sustain tidal flows, and fund green approaches to managing urban runoff. With grants from the CA Environmental Enhancement Mitigation Program, the Friends just purchased 11 vacant lots adjacent to the Slough. Wow! Wetland wildlife benefit from broad buffers.



Once the lands were acquired, the Friends began planting native vegetation and improving trails. Also new are a bridge over the stormwater swale and a kiosk to keep neighbors informed about wetlands, conservation, and restoration. Thank you, Friends, for rescuing this “diamond in the rough” and making it shine.

Restoring for the long-term: Make it big!

Large protected areas are especially needed along the coast, where climate change will accelerate the rise of sea level. A large area would provide room for diverse habitats and their diverse biota to migrate inland as water rises. Areas that are now uplands will be—and will need to be--the coastal wetlands of the future.

At Ormond Beach, there are plans to establish a large conservation area (1,500 acres). The idea dates to at least 2008, when I learned of the project and wrote the City of Oxnard to encourage a large area for the reasons above and more: Large areas support more species by having more habitat heterogeneity. There is room for cordgrass, marsh plains, high marsh, tidal creeks, channels, and transitions (ecotones) toward uplands. Fish use multiple habitats (Larkin et al. 2008), as do birds and other highly mobile animals.

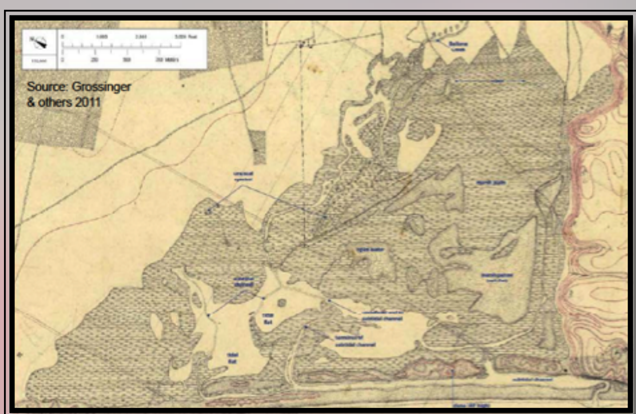
Large areas include more microhabitats that attract a wider variety of species. Note that seed germination differs among species, and small differences in habitat lead to differential establishment of annual plant species. Because temporal variability is high, it takes a large area to ensure that suitable conditions persist in at least some microhabitat (Noe and Zedler 2000, Varty and Zedler 2008).

Large reserves are needed to support species that show negative interactions. Management actions can benefit one species while hindering another. A simple example concerns a predator and its prey. Northern harriers need access to prey, which suggests the need for large open grassy areas, while clapper rails need upland high-tide refuges with shrubs to hide from predators. For a site to support both, it needs to be large enough for both shrubby and open upland habitats.

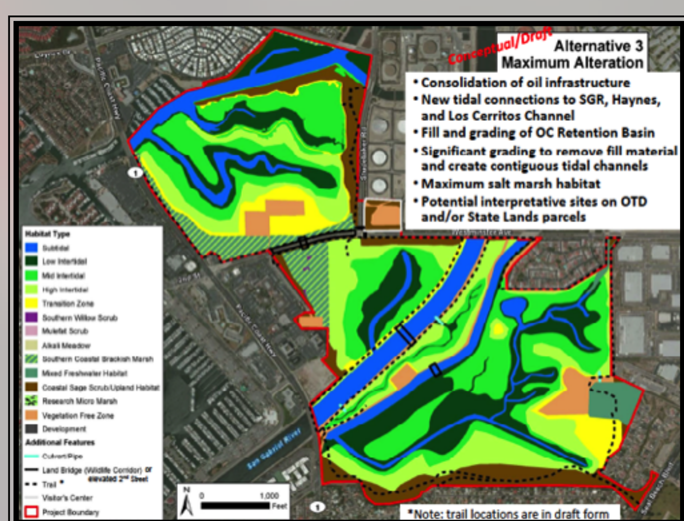
Large areas have room for broad buffers between developed and protect land. Broad buffers are critical for many bird species that are sensitive to nearby activities. Some nocturnal animal species (e.g., lizards) are sensitive to nearby lights; loud noises are disruptive, and distance protects species from noise. Runoff can tip the balance toward invasive plants. With wide buffers, there is more area to absorb inflowing contaminants from urban runoff that might seem harmless. Core areas with broad buffers have higher quality habitat (Callaway and Zedler 1998).

Critical upland habitat is needed to support animal species that provide wetland ecosystem services. For example, uplands support ground-nesting bees that pollinate salt marsh birds-beak, a federally endangered plant (Parsons and Zedler 1997). Inland habitats and shrubby species provide perches and refuges for animals (James and Zedler 2000). Uplands can provide refuges to protect clapper rails that move out of the salt marsh during daytime spring tides in mid winter. Upland animals disperse salt marsh plant seeds. Upland herbivores and carnivores are part of the wetland food web. Larger areas reduce chances that native species will succumb to more aggressive exotic species, such as the yellowfin goby (Williams et al. 1998). Fortunately, more large restorations are being planned for southern California salt marshes.

At **Ballona Wetlands**, we can't restore the area where it existed in 1876 (below, left), because >900 acres is now Marina del Rey. But we can improve ~600 acres that highly altered but restorable. The draft concept on the right is from the 2012 Ballona Wetland Science Advisory Committee discussion. In black are permanent roads; in blue is a proposed, modified flood control channel, which is now a "straight shot."



Los Cerritos Wetlands could undergo alternative restoration efforts, ranging from minimum to maximum alteration (*draft* map from www.intoloscerritoswetlands.org/restoration.php).



This 500-acre site is challenged by oil wells, roads, highways, flood control channel, and industrial development.

It also has a dedicated land trust (www.lcwlandtrust.org/) and active restoration, including an on-site plant nursery. Thank you, Tidal Influence principals, Eric Zahn (below) and Taylor Parker.

When he's not teaching Environmental Science at CSU-Long Beach, Eric might be out restoring wetlands, often with help from his students. Over the years, Eric has revealed many secrets about Los Cerritos Wetlands:

• Its habitats are: Southern coastal salt marsh, southern coastal brackish marsh, alkali meadow, mulefat scrub, southern willow scrub, salt flats, subtidal marine, rocky intertidal, mudflat, and ruderal wetlands, and uplands.

• Its special-status animals are: Belding's Savannah sparrow, black skimmer, burrowing owl, California least yern, loggerhead shrike, northern harrier, pacific green sea turtle, salt marsh tiger beetles, salt marsh wandering skipper, and yellow breasted chat.

• Its special-status plants are: California boxthorn, Coulter's goldfields, sea blite, Lewis' evening primrose, southern tarplant, southwestern spiny rush and woolly sea blite.

Los Cerritos Wetlands were once mostly salt marsh, but large areas are now weed infested or bare--in need of restoration. There's much to do; keep up the great work!

San Elijo Lagoon has a long-range plan that calls for restoring tidal influence. Work is scheduled to begin in 2016 with construction phased over two years to sustain refuges for resident species. The site is a 979-acre reserve that boasts ~400 plant and ~300 animal species. Like Batiquitos Lagoon, the Paci ic Coast Highway (1912), railroad (1920), and Interstate highway (1965) were all built on fill, along with dikes and levees. The site was dissected (cut in two) by Interstate 5, and a concrete dike was built to confine water within the East Basin to create attract migratory waterfowl.

(http://geology.campus.ad.csulb.edu)

Here's what could happen. Shallow-water areas could be dredged in some areas and filled in others to improve tidal circulation; the dike east of I-5 could be opened to expand tidal flow and the area of salt marsh. Lastly, habitats that will experience sea level rise could be connected.

Tijuana Estuary has benefited from several small restoration efforts, and the science of restoration ecology has also benefited where we incorporated experiments to learn while restoring = shorthand for adaptive restoration. The next plan, developed by Chris Nordby, indicates how to restore 500 more acres! Here's the conceptual drawing for one approach, involving plenty of mudflat, tidal marsh, and room for sea level to rise onto transition and upland habitats.

A 500-acre restoration site in a National Estuarine Research Reserve is an ideal place for research, field experimentation, and more research. I am grateful to all those who kept Tijuana Estuary from becoming a marina and to NOAA for designating it the Tijuana River National Estuarine Research Reserve!

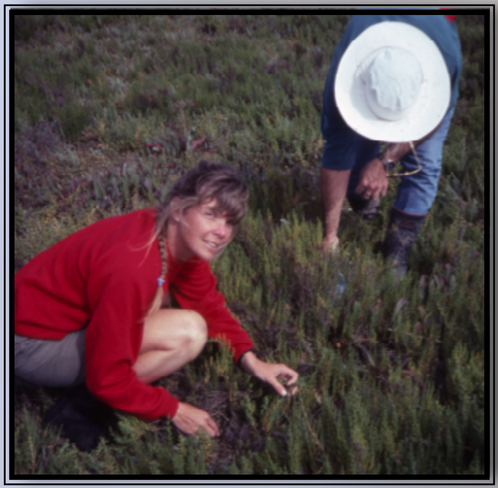
The value of adaptive restoration

Ecological restoration (the practice) makes a lot of progress through trial and error. Way back in 1976, Chris Nordby and I transplanted cordgrass into a former sewage lagoon with black, smelly soil. The first batch of ramets died. We transplanted several more patches and eventually found a "sweet spot" where some cordgrass survived and spread vegetatively. In the process, we improved our skills in collecting ramets, transporting them to planting sites, placing them in new holes, and gaining a sense of where they might survive. The trial-and-error, wait-and-see process had some advantages—it didn't require a lot of planning and we eventually got lucky. The disadvantage was that when plants died, we didn't know why. Now, with more science available, it as probably hydrogen sulfide concentrations that contributed to high mortality.

Restoration ecology (the science) progresses by testing and either accepting or rejecting hypotheses, but a single study that contradicts what others have found might not change opinions. Science progresses by repeated testing and reaffirmation--as hypotheses withstand repeated testing, they gain strength. In ecology, there are many variables that can explain findings. The advantage of hypothesis testing is that we can rule out some factors as not significant, then test others that show promise of explaining outcomes. We can also explain cause → effect by controlling variables.

For example, Ted Griswold (1988) tested the effect of water depth on cordgrass and perennial pickleweed. As hypothesized, cordgrass grew better with water at the soil surface, and pickleweed grew better above the water table. Then, his root-profile experiment explained why: With plants confined to 75-cm, 50-cm, and 25-cm tubes placed in 5 cm of water, the results explained the earlier finding. Pickleweed easily grew down the 75-cm and 50-cm tubes, where they achieved maximum biomass just above the water table. Cordgrass died in tall tubes, but its roots grew well in short tubes at the 20-cm-deep water table. Differential responses of roots to water depth explained why two species are found at lower versus higher elevation.

Adaptive restoration (learning while restoring) combines these two approaches by testing hypotheses in actual restoration sites. In phased experiments, the results of early observations and experiments are used to restore later phases, which provide new opportunities to observe outcomes and test new hypotheses, and so on, until the site is covered with plantings and other manipulations. Here are two examples:



At Sweetwater Marsh, Brian Fink sowed seeds of salt marsh bird's beak on a salt marsh island (trial-and-error). When plants produced few seeds, Lorraine Parsons (left) learned that pollinators were limiting and that we needed to provide habitat for ground-nesting bees (scientific approach). We moved the seeding effort to the "mainland" where there was plenty of supratidal habitat for ground-nesting pollinators, and the bird's beak population thrived.

At the Tidal Linkage, our diversity experiment (chapter ten) tested the need to plant all 8 marsh-plain halophytes. It was clearly not necessary to plant perennial pickleweed, and it was sufficient to sow seeds of two short-lived species (thanks to the scientific approach). Also, that experiment showed greater productivity with species-rich planting than monocultures. However, a decade later, that pattern disappeared (Doherty et al. 2011; combining scientific and wait-and-see approaches). In the meantime, we used the earlier results from the Tidal Linkage (~0.5 ac) experiment to plant the Model Marsh site (20 ac), avoiding species that recruit well from seed.

With new experiments, we tested the need to:

- amend soil in the excavated site,
- plant seedlings in tight clusters ,
- add tidal creeks (benefiting both plants and fish), and
- provide pools (5-cm deep for annual pickleweed; >10 cm for invertebrates [fish prey]).

We hadn't predicted that large pools would form or that sedimentation would recontour the Model Marsh in 2004, but we learned that the geomorphology of a newly excavated site is dynamic. In general, topographic heterogeneity aided ecosystem development. Experimentation led to guidance for the next, much larger restoration efforts that are planned for Tijuana Estuary and other southern California coastal salt marshes.

While we had some difficulty coordinating the site, the staff, and funding, I still recommend capitalizing on the availability of actual restoration sites and using them to test alternative approaches. Our research suggests the several cautions for future restoration at Tijuana Estuary:

• First, large size sites can be a constraint on salt marsh restoration. Simultaneously exposing 20 acres of former salt marsh soil allows salt crusts to form as tidal waters move over the dark surface, heat up, and evaporate.

• Second, seedlings have low survival on hypersaline flats. Under natural conditions, vegetatively reproducing halophytes would creep slowly onto exposed mudflats, or seedlings would germinate in the shade of their ancestors. Tightly-cluster plantings have some advantage. Perhaps a reader will figure out what the advantages are!

• Third, tidal creeks accelerate ecosystem development, but they will fill in or erode, depending on circumstances, including big floods. Creeks might form on their own if the site is excavated to mudflat level. Perhaps all that needs to be excavated is the creek-channel connection. We know that additional creeks formed on their own.

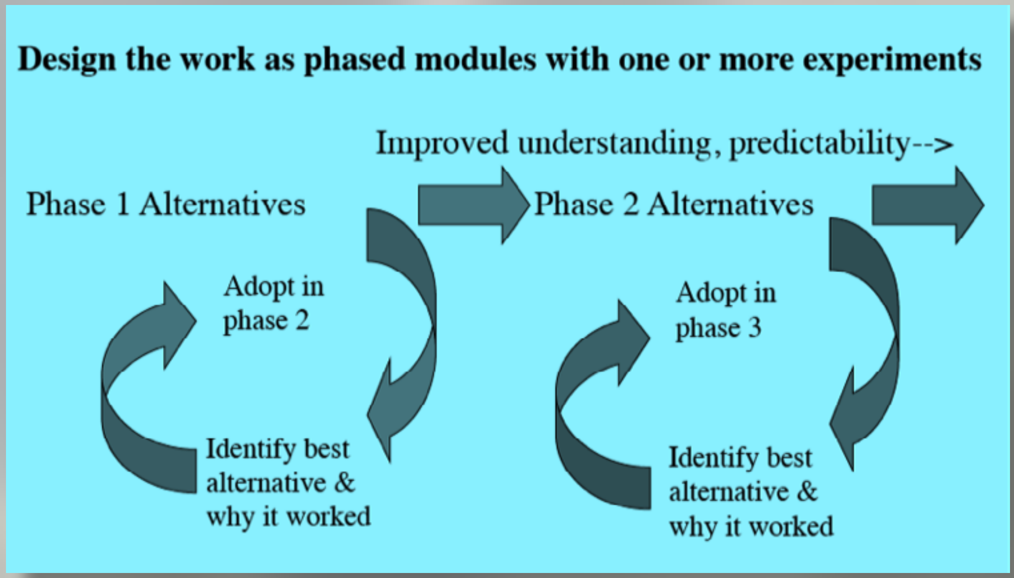
• Fourth, if small islands of marsh plain elevation are left within the mudflat, the marsh plain area that needs to be planted would be small, and seedlings could be planted in dense, mixed clusters to allow rapid canopy closure and prevent salt crust formation.

• Fifth, given plenty of inflowing sediment, the islands should expand as plants trap and stabilize substrate.

Adaptive restoration is a useful approach.

Adaptive restoration combines restoration and experimentation and the accumulation of knowledge. At Tijuana Estuary, adaptive restoration also tested ecological theory while it answered restoration questions and restored salt marsh.

No two restoration projects are identical; each has unique aspects. Even though we wrote a *Tidal Restoration Handbook,* it's still important to tailor our recommendations to each new site and test new ideas wherever possible. A wise approach is to be adaptive, changing the details as needed when new information develops. Frequent communication among researchers and stakeholders is essential.



When should we change our target?

Probably the most difficult decision in restoration is to give up on achieving a target. There was no argument for restoring this house after the Tijuana River cut a new channel at its front door in 1993. There was too much damage on site and no chance of controlling the force responsible.

Ecosystem restoration should aim to sustain all the species in the region and to restore all the services that can be expected whenever and wherever possible. Adaptive restoration is a path forward that helps managers learn what is possible.

I know we can't turn back the clock.

At the same time, I know we can't stop trying. JZ