Salt Marsh Secrets

Who uncovered them and how?

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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:

How do mobile and immobile animals survive salt marsh stresses?

Mobility is the ability to move freely, of one's own accord. The wind can move an organism, but that organism is moving passively (without using energy). It's not mobile unless it flies or swims or walks or slithers (like a sea slug).

A big reason why there aren't many species of vascular plants in salt marshes is that plants are immobile (stuck in one place). Once they establish roots, they can't move up or down the marsh or in and out of the wetland. In the marsh, they have to survive both exposure to warm winds and dry air, as well as impacts of inundation (reduced light, reduced access to carbon dioxide, and soil anoxia). In the wetland, the immobile organisms risk impacts of flooding, sedimentation, sea storms, and herbivores.

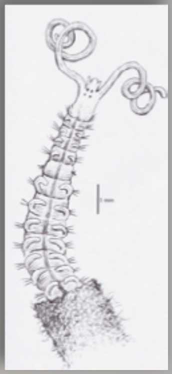
Still, plants have one life-history stage that can be moved: SEEDS. Depending on their size, weight and structure, a seed might drift with the water currents and tides, glide through the air with the wind, or hitchhike on the fur of mammals or in the guts or on the feet and feathers of birds. As long as seeds drift, glide, or hitchhike to a suitable habitat, this is an advantage. But long-distance dispersal is risky; they might land where conditions are uhnsuitable for the seed to germinate or the seedling to establish in a salt marsh.

There are advantages to being mobile. An animal that can move out of the salt marsh or from one wetland to another can escape stress or find resources when its usual home is uninhabitable.

What challenges immobile animals?

Immobile animals are like plants in at least one way: once attached to the substrate, they are basically stuck in that place. Like plant seeds, some offspring (larvae) can disperse passively or swim. Examples of immobile salt marsh animals are bivalve molluscs (mussels and clams) and barnacles. [Although individuals are immobile, they can still be widely dispersed if a few attach to ships and floating debris. If they survive and land in a suitable place, they can reproduce and establish new populations.]

(Photo: Rainer Zanz)



What explains the high diversity of immobile animals that occur in cordgrass marshes? Are there fewer challenges in the low marsh elevation, or are the immobile animals more diverse because they have a different evolutionary history? I think it's their historical origins: marine versus terrestrial.

Streblospio, a polychaete worm
(Illus. McIntire © Zedler)

Salt marsh habitats alternate from aquatic to terrestrial.

When immobile animals are stressed, plants with terrestrial origins (halophytes) thrive. When halophytes are stressed, immobile animals have the advantage:

During high tide, immobile aquatic animals thrive by filtering food from the water and filling their guts to survive the next low tide. Inundation is beneficial—it allows them to feed and reproduce and disperse larvae. Think of immobile salt marsh animals as the landward extension of the marine fauna.

During low tide, the advantage shifts to terrestrial-type species. The salt marsh halophytes that were stressed by anoxic soil during high tide thrive when they have access to carbon dioxide in the air and lots of light (no "shade" from deep water). Think of the halophytes as the seaward extension of terrestrial plants.

Mussel larvae settle on something solid and "stick their landing" by growing byssal threads. How do they cope with "terrestrial" (low tide) conditions? They can close their two shells (bivalves), for a few hours to keep from losing moisture. When under water, they open their shells and suck water into their incurrent (intake) siphon. They absorb oxygen from the water and filter food particles before expelling the "used water" through the excurrent (outflow) siphon. To reproducte, male mussels release sperm into the water and females release eggs. After fertilization, the larvae (called spat) float in water, feed on plankton, grow and disperse. Some mussel species journey afar by parasitizing fish that are highly mobile. Although our native sea mussel (*Mytilus californicus)* and bay mussel (*M. edulis)* do not have a parasite stage, the larger sea mussel is widely distributed on rocky beaches and pier pilings--hard substrates that allow attachment. The smaller bay mussel is abundant in the quieter waters of estuaries, where it grows in clumps on bottom sediments.

It's OK to be stuck at home if you can close your shell and survive low-water stressors (hot dry air). Barnacles "put a lid on" their feeding opening by closing small plates. They can't feed for awhile, but they don't dry out. When inundated, barnacles reach out legs to sweep the water for something edible. Search the internet for "barnacle morphology" for some great images.

What other threats would immobile animals worry about (if they could worry)? How about carnivory by sea otters at high tide and by raccoons at low tide? Both predators can crack mussel and clam shells. As with plants, animals have no strategy that withstands all challenges all of the time. Species sustain themselves (persist) by producing lots of offspring. Species go extinct (none left anywhere on earth) when they are unable to survive or adapt to current stresses.

What secrets did scale insects hide?

Here's a story about an immobile scale insect that was threatened by a carnivorous beetle. Fortunately for the cordgrass and clappers rails, the beetle was usually able to keep the scale insects under control (or at least that's what we think happens).

Kathy Boyer was looking for an MS thesis project when our San Diego Bay study site experienced a scale-insect irruption (population outbreak). I had never noticed this insect (*Haliaspis spartina = H. spartinae*) on cordgrass before, so of course, I wanted to know why it irrupted only in the short cordgrass of the restoration site in Sweetwater Marsh and not in the tall cordgrass of natural marshes? The scale insect was a threat to the restoration goal of growing tall cordgrass for clapper rail nesting (see chapter three).

WAS CORDGRASS SHORT BECAUSE THE SCALES WERE EATING IT, OR WERE THE SCALES EATING THE CORDGRASS BECAUSE IT WAS SHORT? Which was cause and which was effect? Scale feeding → Short cordgrass? Or short cordgrass → scale outbreak in the absence of a carnivore? A reasonable hypothesis was that the short cordgrass prevented the scale's natural predator, a terrestrial beetle (*Coleomegilla fuscilabris)*, from being able to eat enough scales to prevent an outbreak. It was possible that the beetles needed tall cordgrass for a high tide refuge, because Kathy saw them moving up short cordgrass stems, then falling into the water as the tide rose. We tried to cage out beetles using wooden structures, but the window screening shaded the cordgrass, making it difficult to separate shading from beetle exclusion. We couldn't separate cause from effect.

Instead, Kathy focused on our field experiment, where we hypothesized that N addition would grow taller cordgrass and, potentially, attract beetles to eat scales. An alternative hypothesis was that N-rich leaves would *increase* scale insect herbivory and "undo" the benefits of N addition, because various insect ecologists had shown that N-rich plants were readily consumed by insects.

In the photo on the previous page, scale insects are abundant on the leaves but, just above, scales are less plentiful on two leaves with predatory beetles. Without beetles, the scales are dense enough to reduce photosynthesis! In the restored salt marshes, Kathy found eggs of the scale insect (*Haliaspis spartina)* on dead stems of cordgrass. Then, she saw large dispersal pulses in late May and again in late July. However, scales never became abundant in the adjacent natural marsh.

Kathy explored whether N addition increased the abundance of scales in the restored marshes, but she found no evidence that either seasonal or prolonged N addition increased the scale population.

Late in the growing season, plots fertilized with 10 applications of nitrogen over 20 weeks had the *lowest* scale insect abundance. Plots fertilized only in March, April, June, or August did not differ from control plots (no N addition). By comparison, scale insects were never abundant in the fertilized or control plots in the adjacent *natural* marsh. Because N addition *reduced* scale insect abundance, fertilization with N could be used to grow tall cordgrass (Boyer and Zedler 1996).

The alternative hypothesis is that the predatory beetles are absent because the canopy is short. This beetle requires tall plants to move above the water during high tides (high-tide refuges). Where cordgrass is tall, as in natural marshes on N-rich clay soil, beetles likely keep scales in check.

Because the scales are mostly immobile, they could not escape a mobile predator. Note that scale insects stick to cordgrass leaves, but they can still be moved about when their home (live or dead leaf) breaks away from the stem. Eggs that were common on dead stems in winter would have been dispersed by tides and floodwaters in January 1993.

Where cordgrass was short because the sandy soil had too little nitrogen, the scales had no predator. Lacking predation, scales were free to survive and reproduce.

What challenges mobile animals?

A species that can move up and down within a marsh can avoid too much inundation and too much exposure. I've described examples in other chapters:

• Ground-nesting bees dig burrows in the transition to upland and then fly into the salt marsh to feed on the pollen of bird's beak flowers.

• The light-footed clapper rail feeds on crabs and snails along exposed creek banks during low tide and walks onto the marsh plain as the tide rises, or onto the upland transition during king tides. And while its eggs and newly-hatched chicks might not be mobile, their floating nest acts like an elevator to keep them dry (and warmer) as the tide rises.

• Fish swim into the estuarine channels to find more concentrated foods and warmer water for more rapid growth.

• A terrestrial beetle flies into the tall cordgrass to prey on scale insects. It uses tall leaves that poke through the water as a high-tide refuge.

Birds are highly mobile; what challenges them?

Salt marshes support both resident and migratory birds, and even the stodgiest (stay-at-home) resident birds have some ability to move among salt marshes. I'm thinking of the light-footed clapper rail. It seems to thrive within its territories year round, coming up out of the marsh only during king tides and major sea storms. Still, clapper rails can both swim and fly and they are sometimes found outside their normal stomping grounds.

At Tijuana Estuary, the non-tidal drought of 1983 killed large cordgrass patches and dried up the tidal pools (photo below). As the water evaporated, the drought extirpated crabs, worms, and other clapper-rail foods. It also drove out the clapper rails.

I recall that there were about 17 pairs of rails in winter 1984, and then zero after 8 months of non-tidal drought. Why did they disappear?

It is possible that the resident rails became prey to mammals or raptors or other predators. If the rails stayed in the drying marsh, they would not have survived for long. Their prey died, and without food, they would have become weak and vulnerable to predation. It is also possible that they left. Did they move upstream to brackish marshes (which were few and far between) or up the coast to San Diego Bay or beyond? We don't know. We do know that they quickly returned once tidal flushing was restored in mid-December 1984, after invertebrate prey were once again available. The steady recovery of the clapper rail population suggests immigration (moving in from another marsh).

This bird is "grounded" during nesting season

Abby Powell uncovered several secrets of bird behavior while studying Belding's Savannah sparrows (BSS; *Ammodramus sandwichensis beldingi*) along San Diego Bay. BSS is a state-endangered bird. Because it's not as rare as the LFCR, it is not yet recognized as a federally-endangered bird, but it is on the California list of state-endangered species. The subspecies is at risk, especially where predators are able to get into the marsh during nesting season. Small marshes with nearby predators (dogs, cats) make poor habitat, even if the vegetation is suitable. Read on.....

Like the LFCR, BSS does not migrate; the birds spend their entire lives in the salt marsh. They have much less suitable habitat than historically, and their population is in danger of extinction.

Unlike the LFCR, BSS flocks and forages in coastal areas when it is not defending its nesting territories. BSS set up territories that the male birds defend against encroaching suitors. Despite high mobility, they are "grounded" during the nesting season. Still, they fly about to ward of interlopers and to escape disturbances. Without some mobility, they would be "sitting sparrows" (like sitting ducks)—highly vulnerable because upland predators do not respect their nesting territories.

Early in her career, Abby explored the effects of human disturbances on BSS, aiming to offer advice to the California Coastal Commission on the importance of buffer zones around coastal wetlands. Her field censusing and experimentation at Los Peñasquitos Lagoon (LPL) and Tijuana Estuary (TE) led to her MS degree (White 1986).

Abby measured territory sizes and calculated territory density at both salt marshes. In 1986, LPL had more breeding pairs (106) than TE (59) and smaller territories (292 m^2 vs. 602 m^2). What might cause such differences? She compared the vegetation and recorded taller plants at LPL (37 cm) than TE (26), and different composition. There was more salt grass (*Distichlis spicata;* image on right from Purer 1942) and less perennial pickleweed at LPL (27% cover) than TE (56%). Salt grass might provide denser cover near the ground, where the birds like to build their nests. Note that in Abby's later study (above), the nests she found were often in love grass, another low-growing, dense-leaved grass.

Ideal for BSS nesting?

• Saltgrass is a clonal grass that spreads vegetatively by sending long rhizomes underground, using the guerilla strategy. It is common in the high marsh and on dunes, where it forms large dense monotypes.

• Max Busnardo was also interested in saltgrass because it is the primary food for the larvae of a rare butterfly, the wandering skipper (*Panoquina errans*). Max was a keen observer, able to see the long, thin caterpillers attached to the long, thin grass leaves. He could spot several before I could see one. Why do you think the butterfly larvae evolved to specialize on this plant?

PEOPLE DISTURB BSS! To see how people affect BSS, Abby estimated "flushing distances"—how close she could come to a male bird defending its territory (from January to August) before it flew away. The range of flushing distances was 5 m to >100 m, with most birds taking flight within 20-40 m from a person walking.

Her 14 study plots at the two estuaries differed in other factors, such as nearby houses, dogs, and vehicles. Those differences allowed her to compare bird behavior (including males singing to defend their territory). Did birds get used to those background factors (acclimate)? Or did some territories reduce flushing distances? Unfortunately, it was too difficult to obtain enough data to compare types of disturbance, but she did see multiple birds flushing near joggers and radios. Abby found 6 birds that returned in 2 minutes, and 2 that were still away after 5 minutes. More research is needed on how long birds stay away from their territories after various kinds of disturbances. And how do temporary absences affect the interaction among territorial birds. Does the adjacent male exploit his rival's absence?

Obviously, it would be best not to disturb the territory so birds could concentrate on the business of attracting a female, bring food to the nest, and raise chicks! Usually the female bird sticks close to her nest, but if her nest is disturbed, she might abandon it. Likewise, if parent birds are away from their nests for long periods, the eggs and chicks are vulnerable to predators. Large buffers between people (and pets) will be best for BSS. A large buffer would also offer more space for foraging during the non-nesting period (August to January). Birds are still sensitive to disturbance when not nesting. Abby recommended that the minimum buffer should be at least 30 m (= ~100 feet; White 1986).

In 1995 Abby Powell studied BSS breeding habitat in San Diego Bay, where >92% of its salt marsh habitat was dredged or filled between 1856 and 1984. The remaining 94 ha of salt marsh occur as patches that are separated by roads and urban structures. Along with urban development came pets—dogs and cats that like to chase birds, raid nests, and eat eggs and chicks.

The region's larger marshes tended to support larger BSS populations. In San Diego Bay, BSS territories were highly variable in size, ranging 12-fold, from about 84 to 1000 m^2 (that's about 10x10 yards to 35x35 yards). Powell and Collier (1998) banded 277 birds on their territories in 1995, and 45.5% of the banded males re-established those territories in 1996. They didn't leave home!

In 1995, the researchers found 54 territories being defended by males. Of the 54 males, 2 did not attract females, but 5 males each maintained two territories with females (polygamists)! A decade earlier, Abby's MS thesis said "The birds are monogamous…" (White 1986). Most were, of course, but not all.

BELDING'S SAVANNAH SPARROWS THRIVE IN LARGER SALT MARSHES.

Larger marsh areas had higher reproductive indices (estimates, based on bird behavior, rather than actual location of nests. They used estimates, because trampling the marsh to locate nests would have been too detrimental to this endangered bird. They did see 7 nests, however, and 6 of those hatched young.

The researchers found that sparrow territories of different sizes covered all of their study areas except where the ground was bare. The nests they found were built close to the ground within 100% cover of love grass, glasswort, perennial pickleweed or salt wort. Each nest was very well hidden from predators and researchers!

To figure out which marshes produced the most baby sparrows, researchers used bird behaviors and presence of young birds as reproductive indices. Again, using estimates reduced trampling across the marsh. They found that larger marsh areas had higher reproductive indices than smaller marshes.

Many small marshes, like the F Street Marsh (below), are surrounded by urban developments. Breeding sparrows failed to produce any offspring at the smallest marsh, whereas larger areas of habitat without adjacent urban structures appeared to produce more young.

"Hard edges" (roads, flood-control channels, airports) instead of broad, vegetated buffers around small, isolated salt marshes appeared to be suboptimal (not so great) for nesting. What appeared to be best for Belding's Savannah sparrows were large marshes with natural transitions to upland--and predator control.

F-Street Marsh (map from www.oceanforce.org)

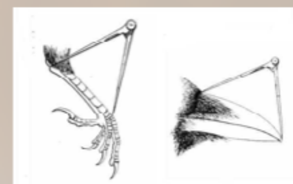
Here's my hypothesis: Small salt marshes surrounded by urban attract upland predators that rob nests.

With today's wildlife cameras, there are more opportunities to monitor nests and determine why some fail to produce young BSS.

Migratory birds: Highly mobile animals

Over 20 species of shorebirds use our coastal sandflats, mudflats, channels, and marshes. Shorebirds are often on the move, walking, running, taking flight, or landing. When do they rest? Are they looking for something or trying to escape something? Or are they just busy interacting?

Finding food and avoiding predators are major reasons for high shorebird activity. Being able to fly, walk, and run uses energy, requiring birds to find more food. Activity might also attract predators, causing flushing and requiring even more energy. In 1979-80, John Boland observed shorebird behavior for his MS research and drew attention to the following patterns:



Tarsus & culmen (wikimedia.org)

• The bigger the shorebird (measuring its tarsus), the longer the beak (culmen). A bigger bird can wade in deeper water and probe through deeper water and sediments.

• Tijuana Estuary supports both smaller species and **bigger** ones (**bold** name):

Snowy plover and killdeer breed and winter at Tijuana Estuary;

Black-necked stilt breeds at Tijuana Estuary, then migrates;

Least sandpiper, western sandpiper, sanderling, red knot, **dowitcher**, **willet**, **marbled godwit**, **long-billed curlew**, **greater yellowlegs**, and black-bellied plover all arrive early and winter at Tijuana Estuary;

Ruddy turnstone, **whimbrel**, Wilson's phalarope, northern phalarope, and semipalmated plover arrive early and continue their migration;

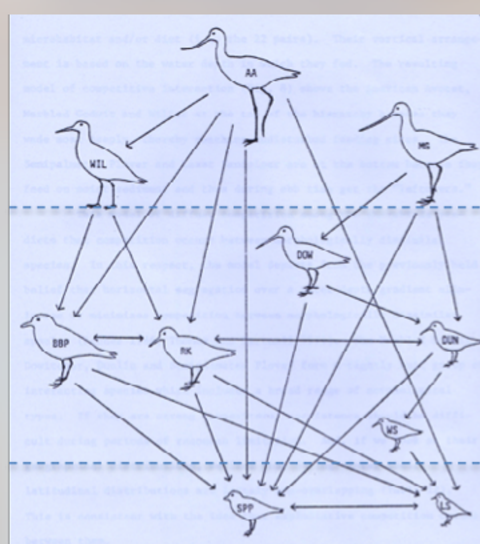
Dunlin and **American avocet** arrive late and winter here.

• Shorebirds feed on similar foods, including polychaete worms, molluscs and crustaceans. Shorebirds tend to feed when the tide is ebbing. Perhaps that's when these invertebrates are most active and visible.

• Smaller shorebirds feed mostly during daylight; big shorebirds take advantage of low tides both day and night.

COMPETITORS OR NOT? Ten shorebird species that feed on sand and mud flats while at Tijuana Estuary might reduce competition by differential wading (bigger birds in deeper water) and differential probing (longer beaks probe deeper). Ecologists might call this resource segregation or complementarity, as in chapter ten. Still, considering that bigger birds feed in the deeper water first, they likely gain a competitive advantage. Resources aren't entirely segregated.

After comparing feeding microhabitats and foods consumed based on data in Recher (1966), Boland (1981) drew arrows between species to show who affects whom. The American avocet, marbled godwit and willet emerged as top competitors (above the upper dashed line). He considered semipalmated plover and least sandpipers to be least competitive (below the lower dashed line).



Small shorebirds fed on the “leftovers” as the tides receded. The birds in between the dashed lines included a range of sizes and behaviors, indicating that competition isn’t necessarily predicted by similar morphology.

Migratory behavior from other records indicated that the middle group wintered in unique latitudes along the Pacific Coasts of North, Central, and South America. High mobility allows shorebirds to form multi-species flocks, share stopovers during migration, *and* split up while enroute to unique wintering sites.

Long migrations north and south can be explained as responses to daylength. Who wouldn’t want to gorge on "all the mosquitoes you can eat" during the Arctic summer, with 24 hours of daylight for feeding? Follow that with a flight south for a tropical banquet after mosquito season.

To be mobile  or not to be mobile? 

(clip art) (clip art)

Mobility and immobility both have advantages.

A mobile clapper rail can move onto high ground during a king tide, and it can return when the tide recedes. Within the region, it can vacate a drying marsh that has lost its tidal influence and return from exile after tidal flushing is restored.

An immobile mussel can close its valves when exposed to the air and open up once the tide returns. While it can be extirpated by lost tidal influence, it can also be re-established by floating spat or adults attached to floating debris.

Likewise, mobility and immobility have disadvantages locally and regionally.

Mobile Belding’s Savannah sparrows can fly off their territories to avoid a threat, but a nearby rival can usurp (take away) some of its territory while it’s gone. At regional scales, entire populations can leave an unsuitable wetland but not find alternative habitats to occupy.

Immobile invertebrates (such as large old burrowing clams) were extirpated from Tijuana Estuary during the 1978 flood, and some species (such as sand dollars) never returned. During regional extremes, such as El Niño storms, new species might expand their distributions from more southern and warmer wetlands and make it impossible for historically abundant species to re-establish dominance in their “home wetland.”

Both mobile and immobile species have persisted for millennia in the region’s estuaries. Can we expect the same into the future? Do you think both strategies will still work with more frequent and more variable extremes of storms and droughts? I hope so.