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).
Layout by Emily L. Rosenthal. Photos by the author or as noted.

PDF name and brief description:

Seasons are the reasons for many salt marsh patterns

Seasons matter to the salt marsh and to the observer. We think of winter and summer as having different weather, especially different temperature and rainfall. In salt marshes, seasons also differ in the tides. Summer and winter have the highest and lowest tides of the year, but their timing makes a difference in what you can learn. If you visit the salt marsh in January, you can see the highest and lowest tides of winter, because they occur in daytime. In summer, you will need to carry a flashlight, because the higher high tides and lower low tides occur at night.

Weather changes with the seasons; so do tides

In north Tijuana Estuary, the cordgrass and succulents are entirely flooded by a higher high tide. Below is a similar view during a low tide. The trestles in both photos once held a pipe that delivered wastewater from the adjacent city of Imperial Beach to a large tidal channel. Those were the days when the "solution to pollution was dilution."

In between the higher high and lower low tides, the marsh is exposed to sunlight, warm temperatures, evaporation of seawater, and desiccation for most of the warm months. Sound like good conditions for plant growth? Yes. Plants require lots of light, and during high tide, the water "shades" the plant leaves.

After describing the tidal and weather seasons, I'll reveal secrets about seasonal plant growth. When do you think the plants are most productive? Or do you think they have high productivity all year long, because they live in a Mediterranean-type climate?

Weather differs over the year because the Earth rotates around the sun on a tilted axis. We have summer when the northern hemisphere (including southern California) is tilted closer to the sun, because sunlight hits the earth more directly and for longer hours than in winter. Seasonal weather patterns are generally predictable. It will be cooler and wetter in winter and warmer and drier in summer.

It is more difficult to predict exactly what next week's weather will be like. To do that, meteorologists rely on computer simulations for a few days at a time. Longer-term predictions are less accurate that short-term simulations. With actual weather data for recent days, the computer operator can recalibrate (set new starting conditions) and improve short-term predictions.

Exercise: Keep track of weather predictions for 5- and 10-day forecasts. See if the meteorologists are more accurate in predicting the daily high and low temperatures (or rainfall) after 5 days versus after 10 days. Note that it is easier to predict weather for southern California's mild climate than for a temperate or montane climate.

Tidal regimes create "tidal seasons"

As the earth rotates, Southern California's ocean waters respond to the pull of gravity from the moon (and a bit from the sun and the earth's rotation). Over ~24 hours, the tides rise when southern California is closer to the moon. The tide ebbs (recedes) when we are further from the moon and there is less gravitational pull.

If you have friends or relatives who don't live near an ocean, they might not have personal experience with tides. They might, however, realize that lake water levels are variable, but mostly in response to rainfall and winds, not the pull of the moon. In Wisconsin, for example, someone living near Lake Michigan will know about seiches (wind-driven water levels), but seiches are not regular like the twice-daily rise and fall of tides. Seiches might suggest to you that ocean waters are influenced by the wind, and of course, they are. A strong west wind during a higher high tide will result in a higher-than-predicted water level.

Oceanographers can predict the effects of the moon's gravity on sea levels (called astronomic tides), but they have difficulty predicting sea swells, which result from storms and varying atmospheric pressure systems (barometric tides). Because actual water levels differ from predictions, oceanographers measure sea levels at tide gaging stations around the world. Deviations from predicted sea levels (anomalies) help us understand the differences between short-term events (sea swells) and long-term gradual changes (rising sea level).

Seasonal tide	Winter	Spring	Summer	Fall
Seasonal **tidal conditions**—National Ocean Service tide tables provide daily water level predictions	Large amplitude; extreme high and low in daylight	Small amplitude	Large amplitude; extremes at night	Small amplitude

"Tidepooling season"

When you live near the ocean, you're probably just as interested in the predicted tide levels as in the predicted weather. If you want to go tidepooling, you need to know about the lower low tides of January, which occur in the daytime.

Tidepooling season is a good time to check out the mudflats of our regional salt marshes. On the right, Abby Powell hosted a field trip during low tide at Tijuana Estuary. That was before there were formal trails to keep people from trampling the salt marsh.

Lower low tides offer shorebirds large mudflat areas to feed during daytime. The shorebirds that are visual feeders need to see their prey in order to capture them. Tactile feeders probe in the mud until their beak feels something to eat. However, they still don't dunk their heads in deep water, because they need to breathe air. [More on shorebirds at: www.fws.gov/oregoncoast/wildlife/shorebird.htm]

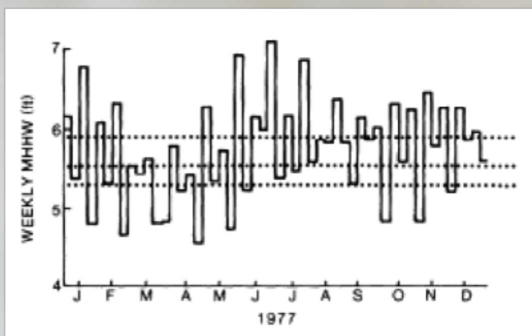
Photo: Lindsay Tudor, Maine

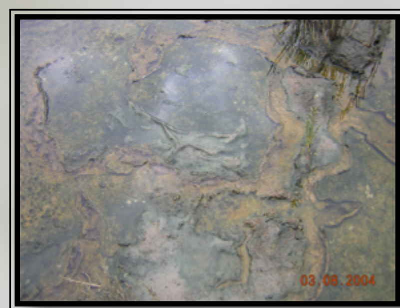
Low daytime tides offer long periods of daylight for mudflat algae (primitive plants without stems or roots) to grow rapidly (more data below). And with more algae, there is more food for snails and worms and crustaceans that feed the birds. All levels of the shorebird food chain ramp up their activities during daytime low tides.

Here's a three-level food chain. It implies that detritus is a producer, but it isn't. Detritus consists of particles of organic matter that plants produce; detritus consists of food that has been partially decomposed by bacteria and fungi:

shorebirds (western & least sandpipers, avocets, willets, godwits, and more) eat
snails, worms, and **crabs**,
which eat **algae** and **detritus**

In 1977, I studied the algae on the marsh soil surface at low (under the cordgrass), middle (salt wort) and high (love grass) elevations. I graphed average higher high tides to summarize when the marsh was inundated at those three elevations (Zedler 1980). The dashed lines represent the three elevations where I sampled algal mats.



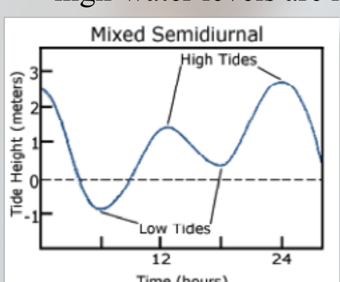


The algal mat is slimy when wet at high tide, but it cracks when it dries out. This photo shows a cracked mat measuring about 30x20 cm.

Algal mats are complex living layers of bacteria and algae, which are abundant in places with plenty of moisture and sunlight, such as tidal pools and mudflats. During drier periods, the biofilm might dry, shrink, crack, and curl up. Watch for signs that the marsh soil has been dry for several days or weeks.

Based on the graph of average higher high tides, what is the longest period that the high marsh would not be under seawater? When would the high marsh be flooded for the longest period? How about the middle and low marsh? How different are the extremes (longest wet period, longest dry period)?

California's tides are called "mixed semidiurnal"—"semidiurnal" because there are two highs and two lows in a ~24-hour period and "mixed" because there is a higher high tide and a lower high tide each day, as well as a lower low tide and a higher low tide each day. By contrast, Atlantic Coast semidiurnal tides have equal-elevation high tides and low tides. Gulf of Mexico diurnal tides (1 high, 1 low) have minimal amplitude (range), and seiches often exceed tides, so high-water levels are hard to predict.



Here's the graph for a single day from the previous chapter. Also, check out NOAA tidal tables (noaa.nws.gov). The average tidal amplitude for southern CA is about 1.2 meter, with the maximum tidal range around 2.4 m. To see how tidal ranges vary, there's a really cool map of global tidal amplitudes (www.nauticed.org/sailing-blog/how-the-tides-work/).

NOAA stands for National Oceanographic and Atmospheric Administration; NWS stands for the National Weather Service. GOV stands for government. NOAA is also the federal agency that designated Tijuana Estuary a "National Estuarine Research Reserve."

NOAA's Tides and Currents station map shows you where water levels and water-currents are monitored. Learn about the tides near you and compare to those along other coasts that you have visited!

The king tide is the highest predicted high tide of the year at a coastal location. It is above the highest water level reached at high tide on an average day. King tides occur when the Earth, moon, and sun are aligned to produce the greatest gravitational pulls of the year. For more about king tides, see www2.epa.gov/cre.

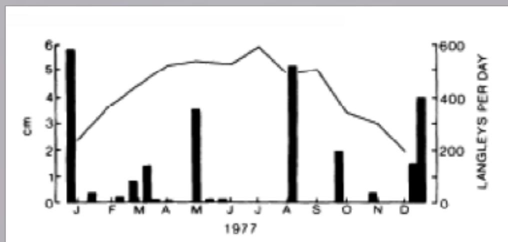
As sea levels rise, today's king tides will become tomorrow's normal extreme high tides—they give us a glimpse of the future's "really high" tide levels. For ideas on how people can reduce impacts of rising sea level, go to another NOAA web site: www2.epa.gov/cre/synthesis-adaptation-options-coastal-areas.

Ralph Tiner explains how tides work in his 2013 book, *Tidal Wetlands Primer: An Introduction to Their Ecology, Natural History, Status, and Conservation.* Dr. Tiner is an expert on wetlands and wetland soils, and he's a very good writer! His chapter on the tides is a very clear introduction, which I will not attempt to improve on here.

"The cool, moist season"

Seasonal weather	Winter	Spring	Summer	Fall
Seasonal **weather**—See National Weather Service temp & rainfall data for Chula Vista.	Cool, moist; intermittent rain storms	Moderately warm, usually dry	Warm, dry	Warm, usually dry

Of course, a rainstorm can spoil a day at the beach or at the salt marsh, so it's helpful to know when it is most likely to rain. Is there a "rainy season"? Some would say November to March—but that certainly doesn't mean it rains often or predictably during those 5 months. There might be no rain or there might be half a dozen storms, some with 2-3 days of rain in succession. Yet it is nearly impossible to predict a month or two in advance just when a rainfall event will occur. Despite this, southern California is reputed to have some of the most predictable weather on earth—that's because you can predict that the general conditions: the weather will be nice, cooler at night, warmer during the day and with little chance of rain. Nearly all of the time, you will be right. Still, some like to say we have two seasons in our Mediterranean-type climate: cool-wet and warm-dry.



This bar graph of weekly rainfall (cm. left y axis) is for Chula Vista, CA (from Zedler 1980). How many weeks had no rainfall? Hint: count the weeks with rainfall and subtract from the number of weeks in a year. This calendar year had unusually widely-spaced rainfall, including late spring and early fall.

The line graph (langleys per day, right y axis) shows monthly average sunlight for Chula Vista. One langley = 1 thermochemical calorie per cm^2.

• Weather refers to the variations in temperature, precipitation, wind, humidity, and barometric pressure. The time period is usually a day or wee. Consult noaa.nws.gov for estimated temperature and rainfall for the next 10 days, as well as records of past conditions.

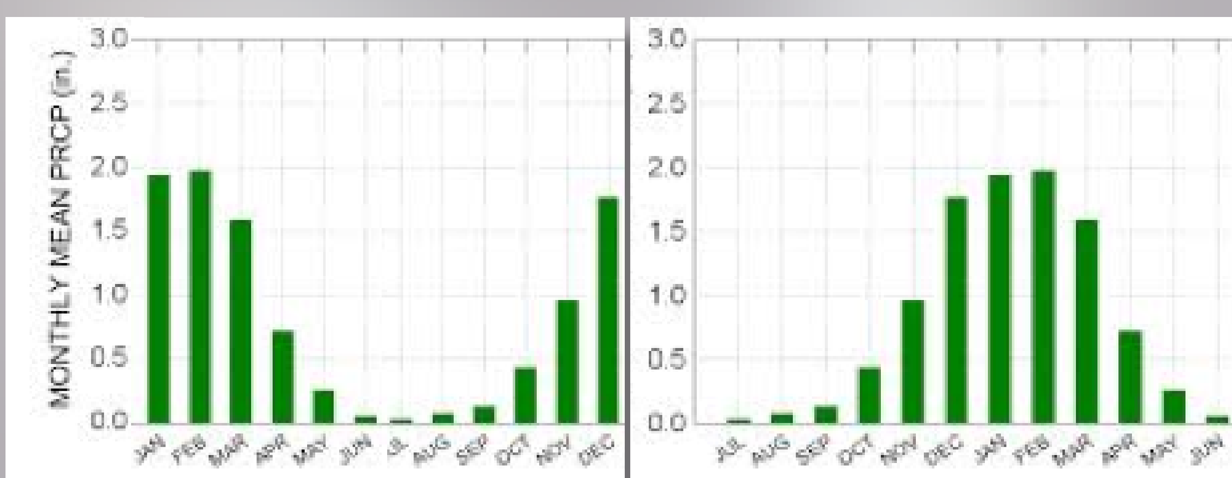
• Climate refers to weather patterns that persist for decades or longer, with one extreme being a tropical (hot-wet climate) and the other an Arctic or Antarctic (cold) climate. Southern California's climate is not too hot and not too cold, but "just right" in both summer and winter. No wonder so many people want to live here.

Rainyears and streamflow years

Years don't always start on January 1. Calendar years do, but rainyears and streamflow years are more useful for some purposes, especially in a Mediterranean climate. If you add up the rainfall for January through December, you will split the rainy period that affects plants and animals. If you add up the rainfall from July 1 through June 30, you will summarize all the rainfall from fall through spring and have a better idea of growing conditions.

Below are the same data (monthly rainfall in San Diego averaged for 1850-2010; www.climatestations.com/san-diego/) presented by calendar year (left) and for the rainfall year (right).

Because it doesn't usually rain in summer, the concept of a rainyear is useful for describing total rainfall. The rainyear covers the cool, moist season by summing precipitation from July 1 through June 30. This makes sense for characterizing the Mediterranean-type climate of southern California. The vegetation grows most actively during the moist period, which extends from late fall through winter and into early spring, so rainfall after July 1 influences the year's plant growth.



In other reading, you might encounter the term, streamflow year, which extends from September 1 through August 31. Riverine organisms respond to the streamflows that begin in fall, so the annual streamflow from September 1 through August 31 can help explain their patterns. Examples are plants that establish seedlings on a sandbar sometime after a flow event deposits sediment; then the seedling either dies or survives, depending on whether there is still enough moisture to support seedling growth. Roots have to reach a dependable supply of moisture before the next dry season with its dry streambed.

Besides day-to-day and month-to-month patterns in rainfall, there are wet years and dry years. From 2012 through 2014, southern CA experienced three dry rainyears in a row. That made life tough for annual plants!

Note: Climate modelers and ecologists expect rainfall extremes (both wet and dry events) to become more frequent and more severe with global change ("greenhouse" warming).

Four seasons of tides and weather

Tides and weather conditions show four patterns over the traditional four seasons. No matter how we draw lines between time periods, we need to remember that local human-made structures (such as flood control channels and tide gates), unseasonal storms (as in April 1983), periodic oscillations of climate and oceans (e.g., the Pacific Decadal Oscillation), and long-term global changes in climate and sea levels can all modify the general, long-term patterns.

Using data from your nearest tidal monitoring station, what were the daily high and low tide levels over the past 2 weeks? Compare the time of the highest high tide in January with the time of the highest high tide in June. Repeat for lowest low tides. If this pattern were reversed, imagine how hot the salt marsh soil would become in summer. Marshes would be even more saline than they area. We measure soil salinity as the water we can press from the soil onto a refractometer that allows us to read salt in parts per thousand. Pure seawater is 34 parts per thousand = 3.4% salt. Salt marsh soil is often well above 43 parts per thousand (4.3% salt).

Seasonal tide and weather	Winter	Spring	Summer	Fall
Seasonal **tidal conditions**—check NOAA National Ocean Service tide tables to find daily water levels	Large amplitude; extreme high and low in daylight	Small amplitude	Large amplitude; extremes at night	Small amplitude
Seasonal **weather conditions**—see NOAA National Weather Service temperature and rainfall data for Chula Vista	Cool, moist; intermittent rain storms	Moderately warm, usually dry	Warm, dry	Warm, usually dry

In winter, it's more likely to rain than in summer. The tides are more extreme (higher and lower) than in the previous fall and the coming months.

Winters along the California coast aren't very cold and summers aren't very hot, but seasons still differ in weather and tidal regimes. Plants respond to seasons by growing robustly during favorable months and resting during unfavorable months, sometimes allowing all their aboveground parts to die and wash away, while roots and underground stems (called rhizomes; photo shows perennial pickleweed and cordgrass) remain alive but dormant (inactive). Salt marsh perennials grow most rapidly in spring and summer (March through September, in response to warm air temperatures and low tides during daylight hours). This tells us that they do not rely on rainfall for most of their water; instead, tides bring seawater to the marsh soil, where roots either exclude the salt (making salty soils saltier) or take up salt, leaving the plant to deal with it.

In the coastal sage scrub, just uphill from salt marshes, plants grow well in the cool moist winter. In between the coastal scrub and the salt marsh is the wetland-upland transition (chapter nine), which isn't regularly covered by tides but does get salt spray and occasional wetting during a sea storm (wind-driven washover).

How the salt marsh functions over seasons

As the tides come and go, the salt marsh changes the quality of the water, and the water changes the salt marsh. Just which things change and how they change depend on the weather and tidal seasons. But even though there are daily and year-to-year differences, the overall pattern is predictable. When do you think the marsh plants start growing rapidly? When do you think they senesce (go dormant, at least above ground). Each flood tide brings water and nutrients and marine organisms from the ocean into the salt marsh and estuary channels. Then the salt marsh changes the composition of the water, removing some things and adding others. Next, the ebb tide carries salt, detritus, floating organisms, and other things from the salt marsh into estuary channels and out the mouth.

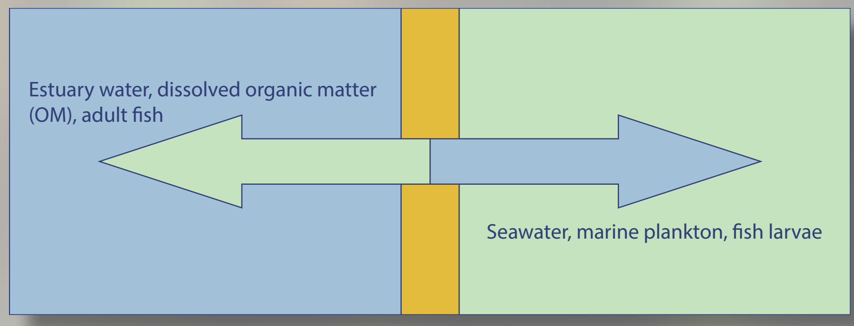
Ted Winfield wanted to know about the dynamics of carbon and nitrogen to compare Tijuana Estuary with Atlantic Coast estuaries that were being described as net exporters responsible for fueling coastal food webs. So, Ted devised a rigorous research plan that taught everyone about salt marsh imports and exports and earned him a Ph.D. degree in 1980. Here you can see where he installed a trestle to support a portable plank so he could collect water samples without trampling and muddying the water:

To measure imports and exports, Ted collected water samples during the rising flood tide and subsequent ebbing tide during 1976 and 1977. In summer, that meant collecting bottles of water at night. Now imagine yourself alone on the marsh next to the city of Imperial Beach and the US-Mexico Border, which wasn't fenced and didn't prevent migrant workers from walking north or bandits from seeking prey. It was also long before there were lights and proper access roads. Sound scary? Ted seemed fearless; maybe being 6'4" tall gave him confidence. I'm sure it helped that he drove a big pick-up truck and brought his German shepherd dog along. Ted's was the first and perhaps still the only study of inflows and outflows of carbon and nitrogen in a southern California salt marsh. It was no small feat!

Because automated samplers were not available in the 1970s, Ted collected and froze water samples as the tide rose to its peak until it dropped to its lowest level six hours later. As if that wasn't enough work, he analyzed over 2000 water samples to quantify the amounts of ammonium, nitrite and nitrate so he could estimate overall nitrogen fluxes (movement in or out). Separate analyses gave him data on carbon content, so he could summarize dissolved and particulate forms.

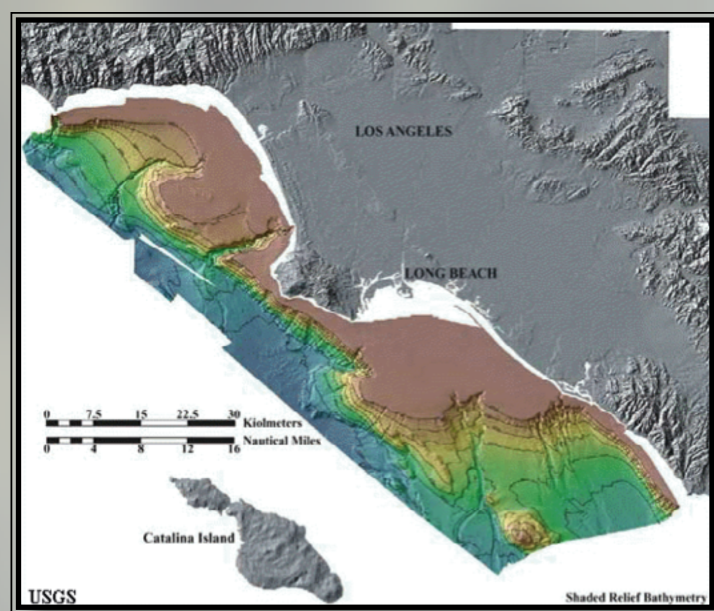
Which brings us to the outcome…..The salt marsh exported dissolved organic carbon, especially in July and January, which have very high tides and large tidal amplitudes—whoosh—out goes the water and everything dissolved in it! Particulate organic carbon was neither exported nor imported. Ted concluded that it was consumed on site, through decomposition (to make detritus) and feeding.

Coastal upwelling of nutrients for phytoplankton.



Simple model of ocean (blue) – estuary (green) exchanges

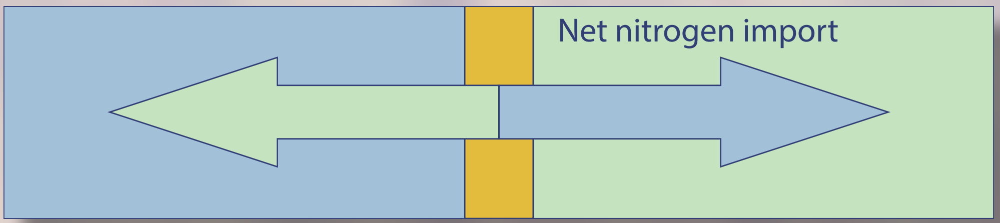
Unlike the Atlantic Coast marshes, Tijuana Estuary was not a major source of organic matter for coastal food webs. Some might consider that a problem based on research elsewhere, but there's an important difference between the East and West Coasts, namely, that the coastal shelf is broad and shallow in the East, while California's coastal shelf (brown in this image) is narrow and steep. Offshore, water currents produce coastal upwelling: Deep ocean water (containing nutrients) moves to surface water, where phytoplankton can absorb enough light to produce food. There, phytoplankton are eaten by zooplankton, which are eaten by fish. Nearshore fish can rely on upwelling, instead of depending on outwelling of particulate organic matter from the salt marshes.



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

The nutrients from upwelling are probably more important to the offshore fishery (fishes that are caught to feed humans or domestic animals) than detritus from coastal estuaries, which are small and widely spaced relative to those on the Atlantic Coast. Highly productive kelp beds near shore also support coastal fisheries; there macroalgae (such as giant kelp) provide both food and structural habitat for fish. Some call them kelp "forests."

Some fish larvae (new hatchlings) move into the estuarine channels and use the estuary as a nursery (a place with plenty of food where larvae can grow fast; see later chapter), but coastal fisheries are not highly dependent on the small, isolated marshes that occupy much smaller areas than the vast wetlands of the East. See NOAA map of coastal wetlands in first chapter.



A “net nitrogen import” means that there was more nitrogen (N) flowing in than flowing out with the tides. During Ted’s study, the salt marsh imported N during the growing season—can you guess why? N flowed into the marsh mostly in the form of ammonium (NH_4, which aquatic plants readily absorb), and some left the marsh as nitrate (NO_3). Ammonium was probably taken up by plants (see Ted’s data for plant growth, below), but some ammonium likely mixed with oxygen-rich water and converted to nitrate.

The net export of some nitrate is easily explained: salt marshes are “leaky systems.” Their environment is “mobile”— and very dynamic. Water flowing in and out takes some nitrogen from the marsh to estuary channels. What else? It also takes dead leaves that might be shading live ones. And it takes away excess salt that plants have excreted (recall the active salt glands). The ability to export salt is important in a warm, dry climate. Without tides to export salt, the soils would become salt flats —which happens in the very high marsh where the sun shines on saline mud for weeks and where tides occur too rarely to remove the accumulating salt. So a mobile environment is good for the salt marsh!

What the plants do from season to season

The flowering plants (those with vascular/water-transporting tissues and flowers, not cones) give the salt marsh its name, because marsh refers to plants that emerge through shallow water. The salt marsh is not known for having gorgeous flowers, but if you look closely, you will see that the grasses are flowering plants, even though their flowers are tiny and have no showy petals. Use your hand lens (magnifying glass) to spot the stamens and pistils. The forbs (non-grasses) are also not very showy; their flowers either lack petals (like the pickleweeds and salt wort) or have very tiny petals.

Sea lavender (photo on right) has a tall, branched inflorescence, but the individual flowers still need magnification to be appreciated as flowers.

The showiest native flower is salt marsh daisy, which has big (well, 2-cm-diameter) yellow flowers. Intermediate in size are the pink-purple flowers of alkali heath.

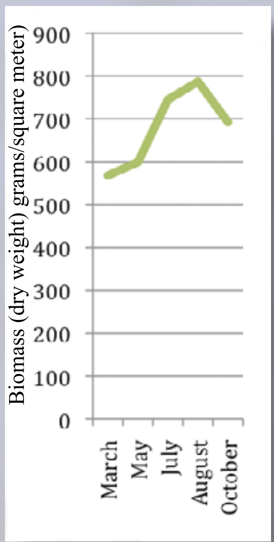
Why are there so few showy flowers? Showy flowers are considered adaptive for attracting pollinators so the plant can form seeds. What do you think pollinates salt marsh plants?

With a moving environment (water currents) and daily wind, maybe water and wind are just as good at pollinating flowers as animal pollinators, such as bees. If so, the plant can save energy by not producing showy flowers—yet still produce seeds. More research is needed!

Ted Winfield wanted to know: When do the plants grow the fastest, and how much biomass do they produce? He learned that southern California salt marshes have lower productivity than those along the Atlantic and Gulf of Mexico Coasts. Stay tuned, however, for an accounting of total productivity, including the algae (nonvascular plants)! Vascular plants are the most visible, but they are not the only plants in the salt marsh!

How did Ted measure the productivity of vascular plants? By harvesting the aboveground biomass every 1-3 months from 58 circular plots (each 0.25-m^2 in area) across the salt marsh, from the low-elevation cordgrass to the high marsh, Ted learned that the plants started to accumulate new biomass in March, reached peak biomass in August, then dropped a lot of their leaves and stems thereafter. That makes sense if you look back to the table of weather and tidal seasons.

In March, tides are not very high; there are long hours of daylight; and the exposed soil warms up. All of these seasonal changes stimulate plant growth. Beginning in March, biomass increases rapidly biomass. All summer long, the lower low tides occur when the marsh plants can absorb sunshine. Marsh soils and plant roots remove some of the nitrogen for plant growth; that explains a net import of nitrogen during summer. August is another period of reduced tidal amplitude, with plenty of warm weather and low tides to support plant productivity. Marsh biomass reaches a peak. Then by late September and October, soils are increasingly saline and growth begins to slow down.



Live biomass at Tijuana Estuary in 1976 (Winfield 1980).

• Light penetration through water: The inundation of the marsh plants by high tides might not seem important, but light is reduced exponentially as it penetrates water. If the water is very clear, 90% of the sunlight might penetrate a 30-cm (~1-foot) layer of seawater. But if the water is murky with sediment and debris and plankton (floating plants and animals), less than 10% of the sunlight might penetrate 30 cm of water.

• It's great to be able to explain data. Some salt marsh dynamics are so complex that we cannot figure them out. For example, how much of a plant's distribution depends on its historical establishment, which might have been a random event, and how much depends on current environmental conditions? How much of a species' biomass is consumed by insects and other herbivores between March and September. We know there are losses to herbivores, which mean that productivity rates are underestimated, but we don't know how large the error is. And how much variation is there in productivity from year to year and place to place (and why)? More research is needed!

Biomass harvesting is "destructive sampling," meaning you clip and remove what you are measuring. Ted sampled every 1-2 months, so he collected biomass even during the nesting season for light-footed clapper rails and Belding's Savannah sparrows. Now, there are strict regulations about entering the marsh when endangered birds were nesting.

What do algae do all year?

In 1977, when Ted was measuring vascular plant productivity, I measured the productivity of the thick biofilms (algal mats) that occurred everywhere on the soil and growing up the stems of cordgrass. They were a rich mixture of filamentous bluegreen algae, diatoms and a filamentous green alga, *Rhizoclonium.* I knew that the Atlantic and Gulf Coast marshes had much taller cordgrass, which absorbed almost all of the light, leaving a very dark soil surface underneath. And scientists (especially Dr. Michael Sullivan, who could identify hundreds of species of diatoms) were finding low rates of algal productivity relative to the tall, dense, light-grabbing cordgrass. Because southern CA had shorter, more open cordgrass canopies, and a marsh plain with a variety of short succulent plants, it seemed that more light would penetrate to the soil surface, stimulating more algal productivity. So that was my hypothesis. Now to test it…..

During my early studies of phytoplankton (at U. Missouri, 1968-69) and lake productivity (at SDSU), I learned to measure algal productivity by comparing oxygen production in light and dark bottles. In the light, an algal mat photosynthesizes and releases oxygen to the water. After incubation in the light, the concentration of dissolved oxygen (DO) increases in proportion to "net community productivity"—a value that is less than NPP because it includes respiration (R = DO uptake) of microbes and animals. Simultaneously, a replicate chamber covered with aluminum foil decreases in DO in proportion to community respiration, which includes all the algae, microbes, and animals. Net community productivity plus community respiration = gross primary productivity (GPP).

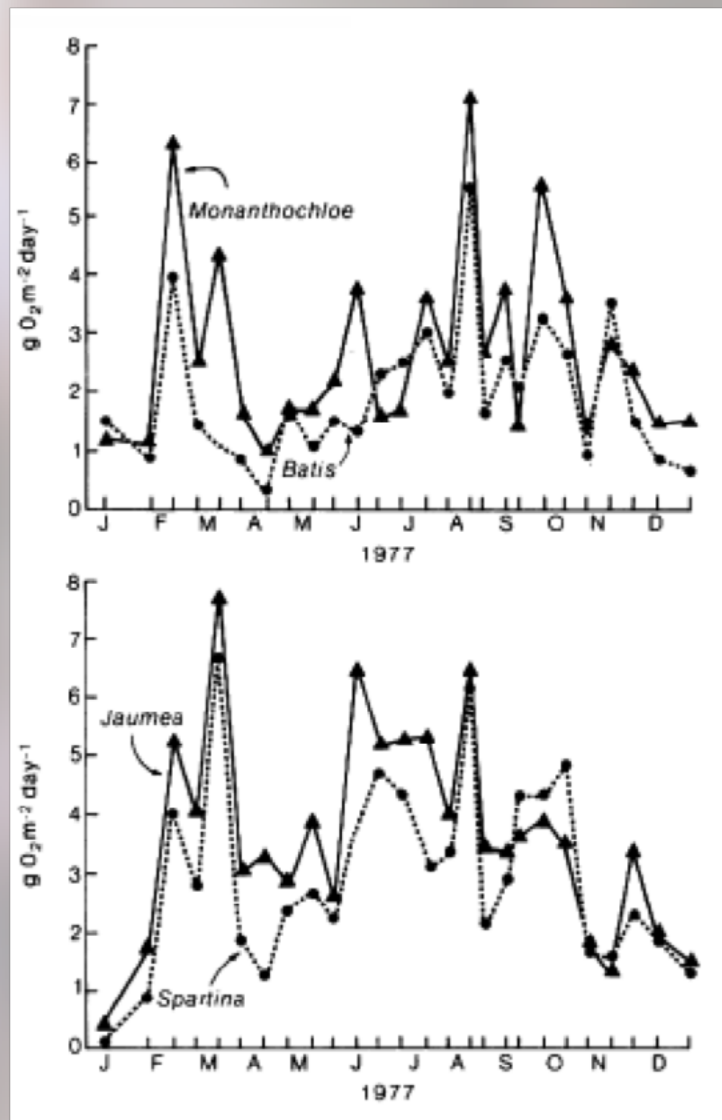
Initial dissolved oxygen (DO) changes x time:

Light chamber measures DO increase = Net Community Productivity

Dark chamber measures DO decrease = Community Respiration

Adding the two changes in DO provides GPP, gross primary productivity, which is proportional to the total carbon fixed during photosynthesis.

I used plastic chambers (made out of clear cylindrical PVC pipe) to cut a disc from each algal mat. I sealed the bottom of the chamber, under the algal mat with a large cork, and I made clear plastic lids that had inflow and outflow tubes. I collected multiple algal mats from the cordgrass, marsh plain and high marsh and covered half the chambers with aluminum foil (“dark” conditions) and carefully filled each chamber with seawater of known DO concentration (< saturated; > 0). It was tricky adding the water without aerating it; I had to keep initial DO constant. I also had “controls” with no mat--to assess any photosynthesis or respiration in the seawater inside the chamber. I placed all the chambers on the marsh surface, in full sun (no shade). Then, after a set incubation time period, I “fixed” DO concentration so I could carry the water to the lab and measure DO for every chamber using a titration method.



Every two weeks, I visited the marsh and set up replicate incubation chambers in four habitats: 1. Cordgrass; 2. Inland of cordgrass in a dense salt marsh daisy canopy; 3. An open, mixed-species canopy with saltwort dominant; and 4. High marsh with the trailing clonal love grass dominant. The extremely variable results were discouraging until several months of data began to show a pattern. Productivity was high when the marsh was inundated at night and received plenty of sunlight during the day—June, July, and August.

Now, recall Ted Winfield’s N data—the marsh tended to export nitrate at those times—probably in part because algal mats were producing bubbles of oxygen mixed with ebb tide water, converting ammonium to nitrate. In contrast, March and April were periods of tidal drought—very suitable for vascular plant growth with infrequent inundation, but less suitable for algal mats, which are essentially aquatic organisms.

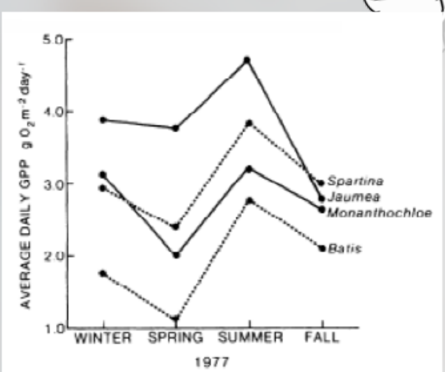
NPP was an unknown value in between GPP and GPP – R, so I had to estimate algal NPP to compare with vascular plant NPP that Ted measured. Which do you think were more productive—vascular plants or algal mats? And were southern California saltmarshes really less productive than those elsewhere? What secret was revealed? Here are the data:

Summary of algal mat productivity under four salt marsh canopy types.

Station:	*Spartina*	*Jaumea*	*Batis*	*Monanthochloe*
1977 Data, n = 25				
Mean hourly GPP				
mg O_2 m^{-2} hr^{-1}	348.4	425.5	236.3	318.9
Coeff. of Var. (%)	(42.5)	(33.0)	(54.5)	(50.6)
Estimated mean daily GPP				
g O_2 m^{-2} day^{-1}	2.84	3.52	1.90	2.60
Estimated annual GPP				
g O_2 m^{-2} yr^{-1}	1,038	1,285	695	951
Estimated annual NPP (NPP = .85 GPP, PQ = 1.2)				
g C m^{-2} yr^{-1}	276	341	185	253
1978 Data, n = 6				
Mean hourly GPP				
mg O_2 m^{-2} hr^{-1}	250.1	279.3	122.0	163.7
Coeff. of Var. (%)	(41.9)	(37.9)	(33.6)	(89.9)

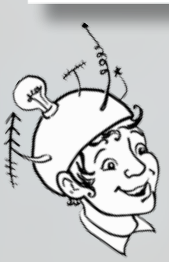
Algal gross primary productivity under four kinds of vascular plant canopies.

A simple summary, after calculating averages for each sampling location for each season, is that algal mats were most productive under salt marsh daisy and least productive under salt wort



Daily algal GPP averaged by season for the four sampling stations. Algal mats are named by their overstory dominants.

In general, the algae were highly productive; in fact, they were just as productive as the vascular plants (halophytes)! I calculated ratios of algae:halophytes = 0.8 to 1.4. (Where algal NPP was equal to halophyte NPP, the ratio was 1.0.) By comparison, a published study from a Delaware salt marsh found an algae:halophytes ratio = 0.33 (algal NPP was only a third of halophyte NPP), and in a study from Georgia, algae:halophytes = 0.25 (algal NPP was only a fourth of halophyte NPP). I hypothesize that the Mediterranean-type climate of southern California and resulting hypersaline soils reduce vascular plant cover, which leads to high algal productivity.



What about total salt marsh NPP? What happened when algal NPP was added to halophyte NPP? A rough calculation indicated that total marsh NPP was just as high as that for East Coast marshes! Southern California salt marshes were not inferior in NPP, Why? Because the algal mats contributed so much more to total marsh NPP.

Another secret revealed. Compared to Atlantic Coast salt marshes, our shorter, more open salt marsh canopies allow more light to penetrate the soil surface, where algal mats can become highly productive. Below is a photo of annual pickleweed seedlings in a shallow depression. The soil surface has a biofilm of diatoms and bluegreen algae.

Because more of the southern CA plant productivity comes from algae, the highly digestible algae would be excellent food for amphipods and other marsh consumers. Algae are highly digestible—especially bluegreen algae. So, the southern CA salt marsh might support more animal biomass than places where vascular plants are the main producers of biomass! That was an hypothesis, awaiting more research. You can see what we learned using newer methods of learning "who eats whom" in the food web chapter.

Now, 35 years later, you might wonder why there aren't more studies of algal and vascular plant NPP in Pacific Coast marshes. Here are two reasons. First, it is a lot of work that requires year-round sampling. Second, the disturbances involved in trampling into the marsh during nesting season and sampling destructively throughout a year are not advisable in endangered-species habitat. Permits are required to enter the salt marsh during sensitive time periods (territory establishment, nesting, brooding, fledging, feeding young). Access is appropriately regulated. Even if a researcher's movements are not disruptive, just tramping through mud to collect algal mats compacts the soil. A single path could drain water unnaturally. I am grateful to the resource agency personnel who protect our wetlands!