

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.

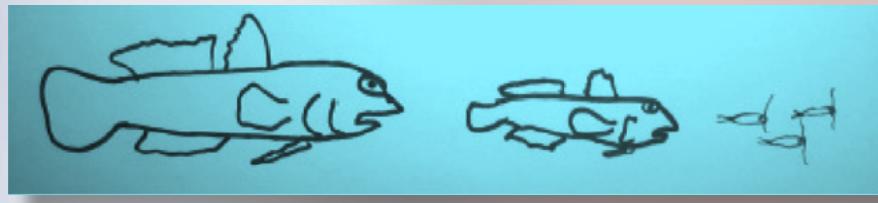
Please download the files as they appear online and enjoy learning what we learned...and more. You'll meet many "detectives," and you'll be able to appreciate how they learned so much--undeterred by mud and flood. *Learn while exploring* the salt marshes near you!

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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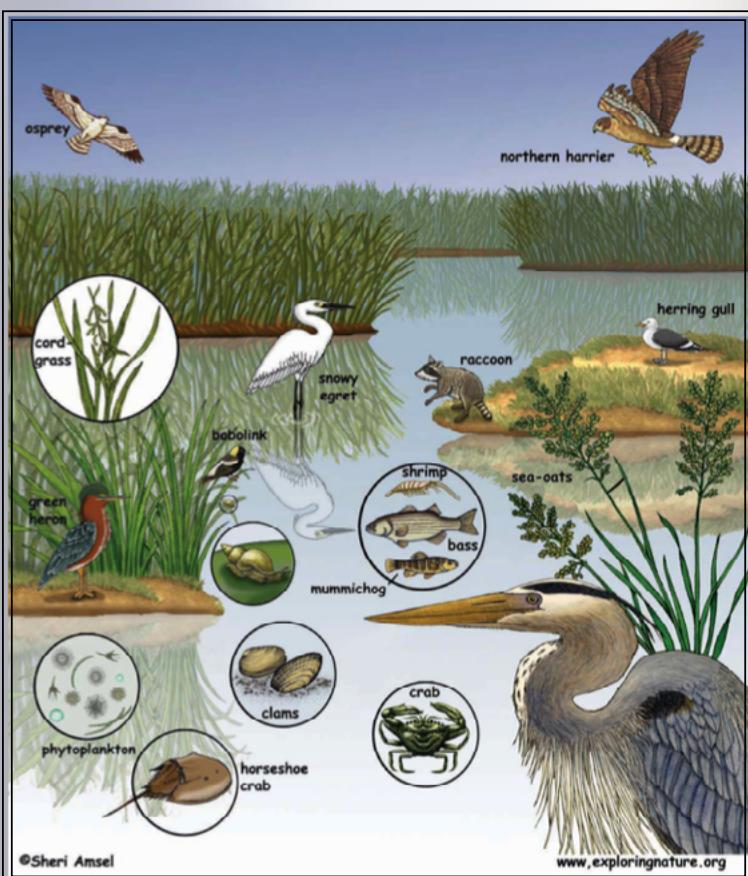
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Who eats whom?



Food webs (**trophic webs**) show the sources of organic matter and the other organisms that depend on those sources. At the base of a food web diagram are the plants that live on site plus any or mobile plankton that move in from elsewhere. Here's a simple **food chain**: plants (**primary producers**) → animals (**consumers**). A bit more specific would be: corn → humans, or grass → cattle (beef) → humans. But few food webs have just one chain, and few trophic levels have just one species. Below is an example from somewhere on the Atlantic Coast, where the cordgrass is very tall and “mummichogs” and horseshoe crabs are present. Can we expect to find the same food web in a southern California estuary?



Somewhat, but with different species and with different food chains becoming important: Recall from earlier chapters that algae produce much more of the food base in southern California salt marshes than in Georgia. Also, more of the biomass produced by algae is digestible, because the algae don't manufacture tough fibers, like cordgrass does. Algae are very important to the southern California salt marsh food web.

Salt marsh consumers include some animals that can eat green vascular plants—for example, a few insects feed on halophytes (like scale insects on cordgrass). Other consumers wait till decomposers attack the tough plant tissues. Fibers and thick coatings on leaves help salt marsh plants resist grazing. So, a lot of the halophyte biomass dies and breaks down into **detritus** before it becomes food for the next trophic level. Detritus is dead organic matter, usually small bits of plant biomass, but also the remains of animals.

In a salt marsh with hundreds of species of tiny animals, it is not obvious what each invertebrate eats or how it interacts with producers. **Peggy Fong** and **Julie Desmond** wanted to know where California **horn snails** (*Cerithidium californicum*) fit in the salt marsh food web. Horn snails are abundant on mud flats. Sometimes they seem to be consuming macroalgae with lush green

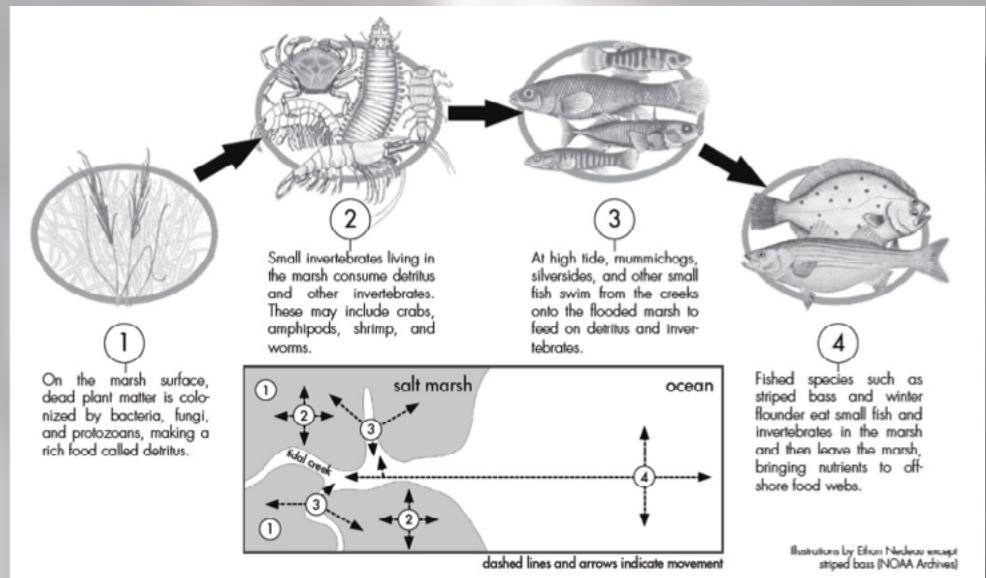


Sowerby.jpg

blades. At other times, it seemed they were the opposite--facilitators of algal growth instead of consumers. Horn snails could be munching away on microalgal mats without damaging macroalgae. While processing cyanobacteria and diatoms, they could be releasing N to the water, stimulating macroalgal growth. How would you figure out which is more likely?

Peggy and Julie set up an experiment in small aquaria where they added a macroalga (let's call it Ulva), then manipulated sediment (a source of nitrogen, N) and snail density (0, 3, 6, or 9 per aquarium). After 21 days, they evaluated Ulva growth and followed the changes in N in the sediment (where it was initially abundant), in the water column, and in Ulva biomass. Without sediment in the aquaria, Ulva grew very slowly, while its N content dropped from 3.5% of dry weight to <2%. Ulva was losing N, rather than growing new cells. There was no evidence that snails were eating Ulva, even when snails were dense (9 per aquarium--the equivalent of 900 per m²). In great contrast, the aquaria with sediment had rapidly growing Ulva with increasing amounts of N in its blades. Where did the N come from? The N in the sediment was decreasing, so the most obvious path of N was from sediment → water → Ulva (Fong et al. 1997).

Why did the sediment lose N to the water, where Ulva could absorb it? You guessed it—the snails plowed over the sediment surface, slurped up microscopic algae, digested them, and released N to the water column. Imagine that—an animal that we thought was eating Ulva was actually facilitating its growth. Before Peggy's experiment, the horn snails had a big secret: Their role as **facilitators of algal growth** was much greater than any role as a consumer of Ulva!



This food web from the Gulf of Maine has **herbivores** (especially insects) that feed on vascular plants and **detritivores** that feed on decaying plants.

The arrows in a food web illustrate paths of [energy flow](#) along food [chains](#) (paths that organic matter takes as it is passed from primary producer to herbivore to top carnivore). Along the way, much of the food is used up ([metabolized](#)) and [lost as heat](#). That's why it takes [a lot of plant biomass](#) at the base to support a few [large fish](#).

It isn't easy to figure out who eats whom, so there aren't many food web models for southern California estuaries. Early work relied on [gut content analysis](#). The web that Drs. Mike Horn and Larry Allen developed for Upper Newport Bay 30 years ago showed mostly short food chains (few trophic levels). For example, topsmelt were shown to feed on algae, making them herbivores. Since then, [stable isotope analyses](#), described a bit later, helped quantify who eats whom. Like Drs. Horn and Allen, we started by analyzing gut contents, but we employed stable isotopes a few years later.

The food web at Tijuana Estuary

Janelle West, Greg Williams, and Dr. Sharook Madon developed the first aquatic food web for Tijuana Estuary channels, using data from the same stations where water quality was being monitored by PERL, beginning in 1987.

As described in chapter fourteen, the team set up blocking nets to trap fishes within a 10-m segment of each monitored channel. Then they repeatedly dragged a bag seine (13.3 m long x 2.1m deep with 3-mm mesh) from one bank to the other. The bag seine had weights on the bottom to catch fish along the channel bottom. It also had a bag in the middle to collect the fish. After each pass of the seine, the team counted the fish. After catching most of the fish, they estimated the total.

Nearly all of the fish that were found in 5 years of monitoring estuary channels belonged to seven species: topsmelt (*Atherinops affinis*), arrow goby (*Clevelandia ios*), California killifish (*Fundulus parvipinnis*), staghorn sculpin (*Leptocottus armatus*), longjaw mudsucker (*Gillichthys mirabilis*), California halibut (*Paralichthys californicus*), and diamond turbot (*Hypsopsetta guttulata*).

Some individuals of each species were preserved for later study of gut contents. The team counted items of food in the stomachs of 579 fish (including 7 dominant species) that they collected from 1994-1999. By summarizing gut contents of fish of small-to-large size, collected over six years, the team also described how fish diets changed with fish age, how they differed among channels and how they shifted over time (from year to year).

For the food base, we lumped together the primary producers and detritus, because it's hard to separate them once food is in a gut. We know the process, but not how much energy flows from producer to detritus before an animal eats a food particle:

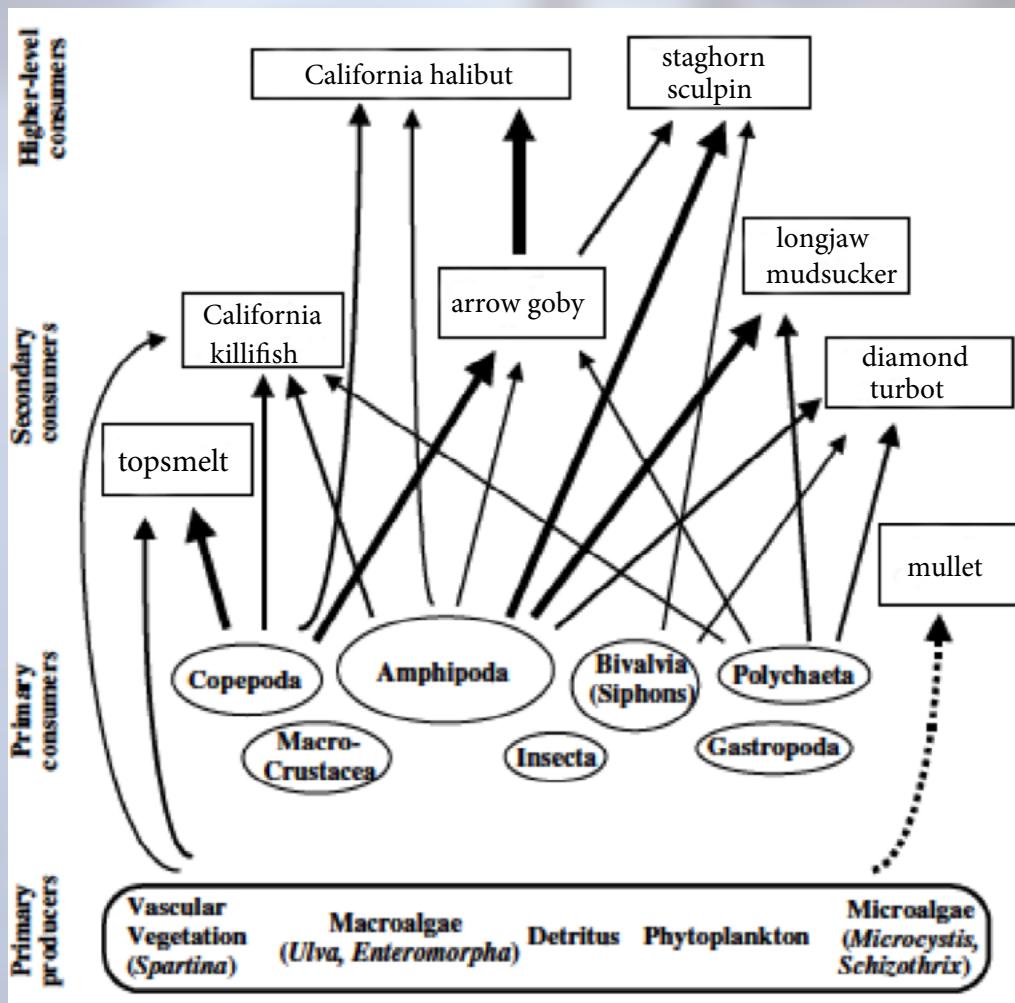
Plant biomass → bacteria and fungi → [detritus particles](#) (globs of plant particles and attached microorganisms). The detritus + microorganisms → zooplankton, which use some of the energy and discard → feces, which add to the detritus (along with feces from lots of other animals). Try drawing a box-and-arrow diagram just for the food base!

Surprise!

Above the food base, there are 3 trophic levels:

- (1) primary consumers--herbivores and omnivores who eat plant material and detritus;
- (2) benthic carnivores--who eat lots of calanoid copepods and an exotic amphipod; and
- (3) piscivores--fish who eat small fish, like gobies.

Also, the team found major dietary shifts during the 1997–98 El Niño floods, when some prey abundances shifted.



Thicker lines
indicate where more
food moves from
prey to predator.

The dashed line
was based on stable
isotope data (Kwak
and Zedler 1997); see
next section of this
chapter.

Tijuana Estuary food web for channels based on gut analysis
(from West et al. 2003)

Many secrets were hidden in the guts of juvenile and adult fish. Only a subsample of fishes that were caught was needed to reveal what each species and each size of fish had eaten recently (and not yet digested). It is hard enough to identify organisms when they are alive and whole; imagine how they appear after being consumed! Identification to species was difficult, so prey were counted in about 33 general groups, such as amphipods and polychaete worms.



Only 79 stomachs were empty; the other 500 had food to sort and identify. Summarizing those data, topsmelt had the most diverse diets with 19 types of prey. Both juveniles and adults are pelagic fish and they ate lots of green algae and calanoid copepods.

Another surprise!

Topsmelt surprised us because juveniles were carnivores! They ate copepods, crustacean and molluscan larvae, ostracods, and insects, while adults were herbivores; they ate polychaetes and bivalve siphons. This shift in animal foods with size (age) is called an ontogenetic shift. In addition, both small and large topsmelt ate algae, which means that their guts had to produce the enzymes trypsin and lipase that digest animal proteins and fats plus the enzyme amylase, which digests complex carbohydrates, like cellulose in algal cell walls.

Diamond turbot and California halibut ate 8 and 9 foods, respectively. Their prey differed, even though they lived in the same places! We call that resource partitioning; the two species can co-exist with less competition by eating different foods. The halibut ate copepods and small gobies, while the turbot did not eat fish. Both ate amphipods, bivalve siphons, and polychaetes. The turbot also ate oligochaetes, copepods, and gastropods. Both halibut and turbot had ontogenetic shifts. The larger fish ate larger prey (details in West et al. 2003).

Arrow gobies are small benthic fish. In this study, arrow gobies ate mostly copepods, plus some polychaetes and amphipods. And arrow gobies, in turn, were prey for larger fishes. The high reproductive rate and short life span of this fish remind me of the annual plants of the salt marsh. Both are “annual species” that can recover rapidly from a disturbance like flooding. The arrow goby also tolerates low oxygen conditions, allowing it to tolerate at least some aspects of a sewage spill. So with various disturbances, arrow gobies fare better than slow-growing, less-tolerant species.

California killifish ate copepods, amphipods, detritus and polychaetes. Their frequently-empty stomachs suggested to Sharook that this species feeds during high tides, rather than our neap-tide sampling periods. During high spring tides, it can move onto the marsh plain and fill its stomach with insect larvae, and marsh gastropods (West and Zedler 2000)

Longjaw mudsucker ate mostly amphipods, especially one that is exotic (*Grandidierella japonica*, from Asia) and also polychaete worms. Staghorn sculpin also ate lots of amphipods but also small gobies and bivalve siphons. Both of these fishes likely benefit from marsh surface pools and a wider variety of prey than we captured by seining in channels.



New ways to learn “who eats whom”

Evelyn Scherr

(known as E. Haines in 1976) made a **major breakthrough** at the University of Georgia, when she began revealing big secrets about stable isotope composition of fiddler crabs, plants, and soils in a salt marsh. She showed that plants and animals “are what they have eaten.” If an animal ate cordgrass that had a specific ratio of heavy and light **isotopes** of carbon (C), then the **consumer retained that ratio** of heavy to light isotopes in its body tissues, which have lots of C (Haines 1976, 1977, 1979, Fry and Scherr 1984). She analyzed the animal’s biomass and learned which plant biomass it had eaten!

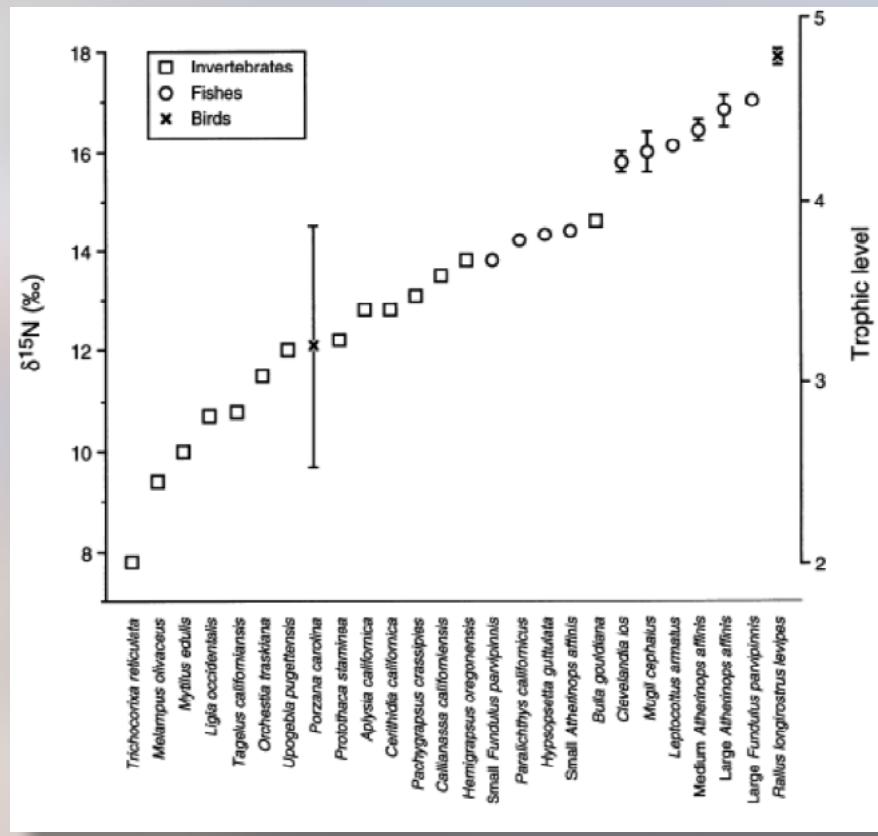
- What’s an isotope? It’s a specific form of an element, like C, N, or S, that with a unique weight. All the atoms of carbon, for example, have 6 protons, but there are three isotopes that differ slightly in mass due to different numbers of neutrons (6, 7, or 8). The three carbon isotopes are ^{12}C , ^{13}C , and ^{14}C . The two that are stable enough to be measurable are ^{12}C and ^{13}C . Note that ^{14}C is radioactive; it decays and is not stable.
- Stable isotopes behave similarly, but they can be separated on the basis of their unique atomic weights. That’s what’s useful to food webs. Different kinds of plants take up heavy carbon (^{13}C) and common carbon (^{12}C) differentially during photosynthesis. By using a mass spectrograph to measure amounts of ^{13}C vs. ^{12}C in a food item, you can learn its secret composition and use that information to see if the next trophic level matches it or some other food source. What a **breakthrough**!
- Stable isotopes of C, N, and S are compared using “delta ^{13}C ” or “delta ^{15}N ” or “delta ^{34}S ” because each is a measure of the **difference** (delta) between a sample and chemical standard for the element being analyzed. The Greek symbol δ stands for delta. Typewriters didn’t have Greek symbols, so we had to write out “delta.” Using carbon as the example: $\delta^{13}\text{C} = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 10^3$ where R is the ratio of $^{13}\text{C}/^{12}\text{C}$ in the sample and in the standard (reference standards were C in PeeDee limestone, N gas in air, and S from the Canyon Diablo meteorite). Dividing the ratio for the sample by the ratio in the standard measures the “discrimination” of organisms in the sample vs. the heavier isotope. Subtracting from 1 makes the difference negative; a greater negative number indicates more discrimination against the heavy isotope. Multiplying by 1000 presents the result as parts per thousand (‰). Ditto for nitrogen and sulfur, with R as the ratio of $^{15}\text{N}/^{14}\text{N}$, or $^{34}\text{S}/^{32}\text{S}$.

Evelyn was the first to use **carbon isotopes** to learn whether the detritus eaten by a Georgia salt marsh invertebrate came from cordgrass or algae; She was also the first to compare the proportions of carbon from various foods that a salt marsh invertebrate ate. Then, she explored the much-debated “**outwelling hypothesis**,” which stated that offshore fisheries along the Atlantic Coast were strongly dependent on detritus produced by vast cordgrass marshes. She collected estuary water and sieved the particles to describe potential food sources. If the sieved-plankton had C isotopes that matched cordgrass, then the coastal “soup” was derived from that salt marsh grass. If it matched the C isotopes for algae in the water, it could be attributed to phytoplankton, or if it was intermediate, the “soup” was probably a mixture. Evelyn found a strong signal from algae. The $\delta^{13}\text{C}$ of consumers was very different from that of cordgrass and more like that of algae. Her results indicated that **coastal fisheries had substantial reliance on phytoplankton**. Another secret revealed! Bravo for algae!

Remember when I discussed C-3 plants and C-4 plants—and how pickleweed's photosynthetic pathway leads to a 3-carbon-chain photosynthetic product, while cordgrass makes a 4-carbon-chain product? Conveniently, these two types of plants also have different proportions of ^{13}C versus ^{12}C . So, in a southern CA salt marsh, we could distinguish consumers of cordgrass detritus (a C-4 plant, with signals of -6 to -19%) from consumers of pickleweed detritus (a C-3 plant, with signals of -24 to -34%), as well as consumers of algae (which have intermediate signals, -12 to -23)!

Later, it became clear that isotopes of nitrogen can show how each consumer functions in a food web, because the ratio of heavy to light nitrogen isotopes increases with trophic level. This finding allowed researchers to tell if an animal was an omnivore who ate plants and animals, an herbivore that ate plants, a carnivore who ate herbivores, or a carnivore that ate primarily other carnivores (often called a top carnivore).

Here are the results of ^{15}N analysis (Kwak and Zedler 1997) showing invertebrates, fishes, and birds of Tijuana Estuary (25 species total). They don't form discrete (separate) trophic levels; instead, they range from mostly herbivorous to mostly carnivorous:



Animals have more ^{15}N in their body tissues when they feed higher in the food web. In marine ecosystems the difference averages around 3.2‰ enrichment of ^{15}N per trophic level.

Researchers also use ^{15}N enrichment to tell if human wastes are used in the food web, because nitrate in wastewater has even more ^{15}N . Why? Because the lighter ^{14}N is easier for bacteria to denitrify, and it volatilizes as ammonia more readily. Those processes leave [more \$^{15}\text{N}\$ in the wastewater](#). Tijuana Estuary has a long history of wastewater spills.

Sulfur tends to be abundant in anaerobic areas, such as [benthic](#) (bottom dwelling) systems and marsh soil, than in [pelagic](#) (deep water) and well-drained systems. Thus, benthic organisms have lower $\delta^{34}\text{S}$ values. This helped ecologists distinguish benthic from pelagic feeders.

How stable isotopes show “who eats whom?”

Attribute	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$:
Enrichment with trophic level	Minimal, perhaps 1‰	Marine trophic levels average ~3.2‰ enrichment per level	Not enriched between trophic levels.
Greatest utility	Indicates plants at the base of the food web. Can indicate whether animals eat in different places at different times.	Indicates trophic position of marine organisms, with organisms feeding higher in the food web having more ^{15}N .	Helps distinguish food produced by benthic vs. pelagic producers and marsh plants vs. phytoplankton.
Reasons why it's best to use multiple stable isotopes to characterize food webs	If two carnivores eat different herbivores or if they eat the same herbivores that fed on different plants, the result would be similar.	^{15}N is not a precise indicator of trophic position, especially where human wastes flow into the system (as at Tijuana Estuary).	$\delta^{34}\text{S}$ values are low in benthic systems that are low in oxygen compared to more aerobic systems.



Using stable isotope methods, Dr. Tom Kwak determined that the base of the food web at Tijuana Estuary is a mixture of cordgrass from the channel edge, microalgae from the marsh plain, and macroalgae from channels. Connectivity among these three habitats is indicated by the mixture of foods from all three habitats. Interestingly, the fishes relied primarily on cordgrass and microalgae, with only minimal contributions of macroalgae.

But wait, there's more. The larger estuarine system had one more trophic level than the tidal pools. Using 3.6‰ for ^{15}N as the “trophic enrichment factor,” Tom calculated that the [estuary](#) had [four trophic levels](#) while shallow tidal pools on the [marsh plain](#) had [three trophic levels](#). In the shallow pools, planktonic cyanobacteria (*Microcystis*) were the [producers](#); next, the surface-swimming water boatman, a true bug (*Trichocorixa reticulata*), was the [herbivore](#), and third, California killifish (*Fundulus parvipinnis*), was the [carnivore](#). The killifish had similar $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values as *Microcystis* and water boatman, but a higher $\delta^{15}\text{N}$ value, indicating that the water boatman was its prey.

I was right!

The Tijuana Estuary food web differs from that of tidal marshes along the Atlantic and Gulf Coasts by having greater reliance on algae. This is consistent with my 1980 conclusion that more of the food base (primary production) in southern California salt marshes is contributed by algae. When I measured epibenthic algal production in the Tijuana Estuary salt marsh, I calculated that algae contributed between 76% and 140% of the vascular plant NPP (Zedler 1980). That was much higher than found for Georgia salt marshes at a similar latitude.

Intertidal macroalgae, marsh-surface microalgae, and cordgrass are abundant in tidal channels, low salt marsh, and mid habitats. Together, they are the primary producers that capture the energy of the sun and make it available as organic matter for invertebrates, fishes, and light-footed clapper rails. Please note that we did not harvest a bird to analyze isotopes in its tissues; instead, we took advantage of a dead rail that the NERR manager had found.

The food-web analyses indicate that the salt marsh and channels jointly support consumers. So, we need to manage these habitats as a single ecosystem. Restoration of endangered bird habitats should not compete with restoration of coastal fishes. In other words, restoring intertidal marshes is compatible with enhancing coastal fishes.

Why do we need trophic level info?

Way back in 1970, Dr. Stuart Hurlbert had an idea that the number of trophic levels could determine whether a pond has clear water or a phytoplankton bloom. Stuart is a limnologist (one who studies aquatic ecosystems). He tested his idea using artificial ponds (2-m diameter, 30-cm deep plastic wading pools), which he set up in full sun on the roof of SDSU's Life Sciences



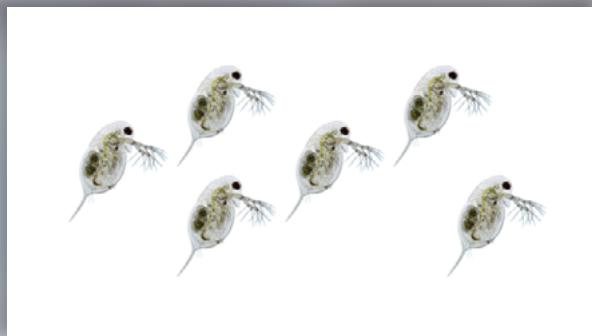
Building. Next, he added 3 cm of sand and filled the pools with tap water. For nutrients, he added a liter of alfalfa pellets (alfalfa has lots of N because its roots harbor N-fixing bacteria). For plankton, he added an inoculum (unfiltered water sample) from a nearby lake plus a zooplankter (*Daphnia pulex*, photo from pixshark.com) from his laboratory culture. My role was to monitor the microscopic phytoplankton. Stuart monitored the zooplankton and insects at the water surface, and Debbie Fairbanks (Stuart's graduate student) tracked chemical and physical factors.

After 3 weeks, Stuart added 3 mosquitofish (*Gambusia affinis*) to 3 of the pools. Those 3 predatory fish (top carnivores) ate *Daphnia* plus rotifers, crustaceans, and insects. When the fish had reduced the numbers of zooplankton, the nutrient-rich ponds quickly developed algal blooms. I had a hard time believing that a milliliter of water could contain over a million unicellular cyanobacteria, so I recounted, and the numbers were correct. But it didn't take a microscope to see that pools with no fish had clear water, while pools with fish were pea-soup green.

The algal bloom decreased light transmission and water temperature, and the water chemistry (dissolved components) shifted from being rich in inorganic phosphorus to being rich in organic phosphorus. Adding just 3 carnivorous mosquitofish changed our pond ecosystems....

With two trophic levels, herbivores and producers, the phytoplankton remained at low levels. Adding a third trophic level (carnivores) reduced the zooplankton, and with fewer zooplankton, the phytoplankton bloomed.

Clear water with lots of phytoplankton-eating zooplankton:



“Pea soup” with fish eating the zooplankton that were eating the phytoplankton:



Hurlbert et al. (1972) were first to test how manipulating trophic levels could control phytoplankton blooms. Stuart speculated further that the effect of mosquitofish could be reversed by adding a piscivore (fish-eating fish). He also described an experiment in Clear Lake, California, where a small zooplanktivorous fish was added to feed on phytoplankton and the larvae of a pesky gnat that made the lake unpleasant for people. Our 1972 paper appeared in the premier journal, *Science*.

Stuart called it “biological control of phytoplankton.” Over a decade later, Dr. Steve Carpenter at UW-Madison published a similar idea, which is now called a “trophic cascade.”

Regardless of who got credit, Stuart’s final words are still relevant: “...fish deserve a higher place in the conceptual schemes of eutrophication research than they are now accorded.”