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[ANNOUNCER:] Welcome to HHMI's 2016 Holiday Lectures on Science. This year's lectures--Ecology of Rivers and Coasts: Food Webs and Human Impacts--will be given by Dr. Mary Power of the University of California, Berkeley and Dr. Brian Silliman of Duke University. The second lecture is titled "Untangling Salt Marsh Food Webs." And now, Dr. Brian Silliman.

[Applause]

[SILLIMAN:] Thank you very much. First, I'd like to begin by thanking the Howard Hughes Medical Institute for both the invitation and support in putting together these lectures and to thank you, the students and the teachers, for engaging with us in this science process, not only in understanding the lectures and discussing that, but in the activities afterward. These interactions are really important for progress in learning and science.

And I'd like to start out today with two take-home lessons that I think are really important from this lecture. I'm going to present a story of scientific discovery, sprinkle in a little bit of drama because everything's not cut and dried in science. And that is that the power of experiments are really important in understanding cause and effect relationships, no matter what field you're in. In mine, it's helped to unravel strong top-down forces in salt marsh food webs, pinpoint those, and then use that understanding to help conserve these ecosystems.

The second one is that science is fun, exciting, investigative, and creative. And when I was your age, I was looking for something like that in a career. And my arrow pointed to history because when I was in those classes, there was a lot of debate. There was a lot of discussion, evidence. I liked science, but a lot of it was memorization. And it was not until my fourth year of college that I started to do investigative science, just not test. And I want to encourage all you guys to do that soon as possible if you want to test out science because that's where you get the creativity and the excitement, is coming up with your own recipe and your own question.

In today's lecture, I've organized that around four different questions. What are coastal wetlands? So I'm going to begin with a natural history overview. What organisms--what are the plants and animals that lived there? How do coastal wetlands benefit humans? What are the services they provide us? And what controls coastal wetlands? What are the ecological forces that do that?

Coastal wetlands are renowned across the world as one of the most highly productive ecosystems--very luxuriant in the amount of plant production that'll come out of that ecosystem in one year. And they primarily develop in protected areas like you would find here in this embayment. And if you look across a gradient of wave stress, you see how important it is for the protection from those waves for these wetlands to emerge.

Here along this rocky shore, this is where we have high wave stress in the environment. And in that system, there are so many waves that the sand and the mud can't settle out. As we decrease the amount of wave stress coming into the system, the sand that's been entrained in that water will fall out, and you get the formation of beaches. But there's still enough storms and wave action to rip up any vegetation if it starts to grow. In these areas, where it's more like a bathtub--we really don't have waves, and they're not very common.

Well, all the sediment starts to fall out, and we get this fine, muddy silt in the environment. And that's where these lush intertidal grasslands can start to develop into these areas. They still need that seawall of protection, though. Where do they get that? On the East Coast of the United States, we don't have the mountains along the coast. What we do have are vacation spots, the barrier islands. And this is an effectively long natural seawall that extends from the Florida coast all the way up to the Jersey shoreline.

And behind that, we have a wave-protected zone. And in those areas, we have development of sediments, intertidal grasslands. And they can be as expansive as 7 miles in width along those areas. They're bounded on this side by wave stress and on this side by freshwater inputs. That allows freshwater plants to come in and outcompete them. So they can't move further inland. On the polar expansion, they're limited by ice. During those winters, it'll grab that grass and rip it up. So they can't go too far to the north.

And in the south, they're limited by competition by bullies, these trees that grow up in the intertidal zone in protected areas. So in the temperate zone in protected areas, we see these lush intertidal grasslands. And that's the ecosystem I want to talk about today. They are also bounded over sort of shorter spatial scales. And if we take a sliver of that salt marsh, we can see how the tide really influences what you find in those ecosystems.

Here's the cross-section of the salt marsh. And here are the different elevations of flooding between a low and high tide in the environment. Here's the mean low tide, and here's the highest high spring tide in the environment. The plants can't go lower than mean low tide because they'll drown, and they can't go higher because again, they meet up with the competitive bully. They can't go in the terrestrial environments. They're outcompeted by those trees, which can't go into here because of the salty environment.

Those tides also create striking gradients that are predictable in the amount of stress the organisms experience in that system. And that stress predictably varies along that tidal gradient. Coming down the tidal gradient in the lower portions of the marsh, we have increasing oxygen stress. There's lower amounts of oxygen in that soil simply because that soil is underwater for a longer period of time. It's difficult for the oxygen to percolate in those soils. So those animals need adaptations and plants for low-oxygen environment.

In the higher reaches, we have higher salt stress. This is not necessarily intuitive. But what happens at the high levels is you only get flooded in those areas one or two times a year. It brings in salt water. And over the period in between the flooding, we have evaporation, so you get concentration of salts. It's more like a desert environment in that. So we have increasing salt stress as we go up.

Now, along these gradients, we also have striking zonation of the organisms in these environments. And what's so amazing about the salt marsh organisms, the plants and animals that live there, is not--you will not be overwhelmed by the diversity. It is not like a coral reef. And sometimes, I wish I was in a coral reef because I want to see diversity.

What you're overwhelmed with is the amount of organisms that fall into your boots. The sheer abundance is just overwhelming, especially when you go up to large spatial scales and think about how many organisms are there.

So here are the plants. And up in this salty or desert-like environment, you find succulent plants, like you would find in a desert. Those are very conservative with their water budget. And then we find terrestrial-like plants on the border. Down in this low zone, we have grasses. And this looks like an agricultural field you'd find in the Midwest. These grasses are among the most productive ecosystems in the world. They rival that of tropical rainforests. They can grow to 9 to 10 feet tall in one growing season in the south. It's about this tall, and it's like walking through a forest of grass--so very productive and abundant in those systems.

The animals in the system, like the mollusks, are equally not as diverse, but super-abundant. And the snails, they occur in the high intertidal system like this. These are periwinkle snails like to climb up the stems of the plants as the tide comes in to avoid predators and continue to graze on the plants and algae that's on them. And then they come back down as the tide recedes to graze on the mud flat.

These mussels occur in super high densities here underneath the plants and act like hot spots of--it's almost like a little spa. They keep more water there. There's less salt. They're like tree fertilizer stakes. They filter water, and they deposit feces right there and can enhance plant growth. These snails can occur 100 individuals per meter squared. Once you get a kilometer squared of marsh, it's 50 million snails. And crabs will also occur in this abundance.

Fiddler crabs are one of the most common crabs that we see in this environment, and they're very cool engineers. They dig holes in the marsh to avoid predators when they come in. They go into those holes, and they just found out they plug them. They don't let the water in. They have a scuba tank of air in there because they breathe oxygen better in the air than they do underwater. It also enhances plant growth. Their densities can equal, if you scale it up to about a third of an acre, the size of a typical suburban house lot, you're talking 150,000 crabs in your yard. And that means everybody in the neighborhood has 150,000 crabs. It's an amazing amount.

And we also have crabs that are predators. These are the blue crabs, one of my favorite things to eat. And these are predators that come in with the flood tide. They're swimming crabs that can go over the marsh grass, and they come in, and they're scavenging, gathering crabs, eating them. They can eat a snail in 15 seconds. So they do a lot of consumption over a short period of time.

Well, the food web doesn't stop there. We have our plants. We have the animals eating algae. And then we also have predators like these blue crabs. And we have predators above them. Here's some of those examples. We have sea otters that are just now expanding--this is very exciting--into salt marshes in California. Alligators that I found out, like, ten years ago occur in these marine systems and love to eat blue crabs. We have bonnethead sharks that are coming up, co-occurring with climate change and the warming of waters in North Carolina.

So all these animals are there. And if you multiply this vast abundance of organisms by the huge size of this ecosystem, there are over 4 million acres of salt marsh just in the United States. You get a generation of very important benefits and services for humans.

One of those is near and dear to my heart. It's a model system for ecology. It doesn't serve as many people but scientists. This is like a dollhouse for doing food web ecology because I can manipulate things that are small. I can change the level that they're on. I can change the number of them in small cages. It's not like working with a lion. A blue crab will pinch you and bite you and injure you a little bit, but it's not anything lethal. And the cages can be a lot smaller. So you can ask questions that are potentially generalizable that you can't, for instance, in a tree system. And the organisms are also short-lived.

They also sequester carbon. We care about taking carbon out of the atmosphere. They're areas where we have high fish production. It enhances commercial as well as recreational fisheries, they protect our shorelines, and they filter pollution. I'll explain these four in the next four slides. Carbon sequestration--there are markets that are about ready just to open up where you can pay for carbon pollution. And the preservation of salt marshes, we contend, should be in that market. If you look at the amount of the carbon burial right here on the y-axis, on the x-axis, are ecosystem--this is a log scale.

What you see is that salt marshes are about 10 to 20 times better at burying carbon over a period of time in comparison to forests, which we're most interested in this. And notice, all your marine ecosystems are here. We call this blue carbon. And the reason that happens is because these plants are fixing carbon through photosynthesis. They're building roots.

But because there's no oxygen or little oxygen in the ground, they don't decompose, and you get a peat layer that's growing over time. It's building up, and it's a carbon bank. They're also what I like to call food factories. These grasses are like big fences. They keep the predators out, and there's a lot of food. It's a good place for small organisms to hang out and grow fast.

And with the expansion of salt marshes and greater area of salt marshes in areas, we see a strong correlation with an increasing amount of important fisheries, small commercial fisheries like drum, shrimp, and blue crabs. And this data right here shows this positive linear relationship. With increasing area of the vegetated estuary, specifically salt marshes, we have a positive association with increasing number of shrimp that fishermen catch in their nets. It's really important because it boosts the local economy.

What about shoreline protection? This is kind of hot off the press-- this is over the five or ten years we're seeing. Can living shorelines, instead of putting up these bulkheads, protect our shorelines just as well under instances of moderate wave stress? And the answer is yes. We've done experiments. The marsh has dampened the wave stress, and they keep the sediment there in its place. That's very important if you're a local landholder, and you don't want to lose your land in that environment. And when you use marshes and oysters instead of the seawall, you not only get protection; you get added benefits. You get fisheries protection. You get carbon sequestration.

So it starts to add on; these living shorelines do an important service in these environments. They're also filters. They're sponges that suck up pollution that is especially coming into these estuaries where we have a lot of human development and runoff. And some of those pollutants that come in there include nutrients: nitrogen and phosphorus that you use--many people use in their yard, a lot of that runs off into these estuaries.

There's also heavy metals, for instance. As they pass from the urban environment before they get into the estuary, they have to go over all these salt marshes. And those plants take up those nutrients. They fix in the organic carbon. They can put it in the food web. And they can lock down some of those heavy metals--so important services like that.

So this may have you begging the question. I started earlier--this is a very stressful system with few organisms, yet has the paradox of being super-productive. How is that the case? So we asked this question, and it's something that salt marsh scientists have been studying for a long time. And one of the hypotheses they've looked at and that actually has a strong support, is that for those organisms that have adapted to that stress, there's a huge bonus.

It's called the tidal subsidy. And this tidal subsidy--this is taken from one of my favorite places on earth, Sapelo Island, Georgia. You see this luxuriant production I was talking about before. This is the grass in Georgia that gets about 9 feet tall by the end of the growing season--really expansive ecosystem here, oysters along the creek bank. This is a picture at low tide. They have 3-1/2 meter tides. And when that tide starts to come in, it's bringing oxygenated water. And that's bringing oxygen percolating down to the roots. It's bringing in more plankton for the filter feeders. And it's taking away some of the toxins that can start to build up: the sulfides that give it that egg smell.

And we have found that with increasing amount of flushing, not surprisingly, you have increasing what? Increasing amount of grass production. So there is a strong tidal subsidies in the environment. And we've looked at other physical factors that could control marsh production because these salt marshes are built on the foundation of plants. We call them foundation species.

So how they go, the ecosystem goes. So as ecologists, we're interested--that's a focal species. It's creating the ecosystem. What are the factors that control its success? And we found a variety of physical factors are very important. I've talked about salt and oxygen. One that's really important is nutrients. And we found, by taking plots, sprinkling nitrogen on versus phosphorus, that this system is very nitrogen in need. It's nitrogen-limited. If you sprinkle nitrogen on there, the grass really grows, just like your back yard. So it's limited by those nutrients.

The sediment type, river inputs, and all these other physical factors can regulate how much nitrogen is in that system. And combined, ecologists--we call these examples of bottom-up factors that can regulate plant growth, nutrients and nutrient-regulating factors. And those nutrients can have a positive effect on plants and resource availability. And if you put this into a very simple conceptual model, ecological model, here we have our plants, who are our primary producer in the system. And the amount of nutrients and water and oxygen available to those plants will be a good predictor of how many plants and biomass and population of those plants you have in that system. Well, we also know that food webs are more complex than this. Plants, many times, get eaten. And so let's--that can be controlled also from the top down. This is a dramatic example of top-down control.

This elephant has ignored the grassland, is going for the good stuff in the trees. They're knocking down that tree and then eating the limbs. That's a lethal interaction with the herbivore. It's killing that plant. And these elephants can have a strong effect on how many plants are in the environment. And we call that top-down control. That's a negative interaction right there. It's making that box even smaller.

If we overlay those together, we're starting to get a conceptual model looking at the relative effects of bottom-up and top-down forces. We have a plant in our system limited by bottom-up as well as top-down effects. And of course, like plants, herbivores can also be limited by the amount of things--the resources, the food that they're bringing into the environment.

In these systems, we also have three levels, in many cases. And that's a predator. We can add a predator to the system. And then, like plants, herbivores can be limited either from the top or the bottom up. In these systems, predators can exert strong top-down control in herbivores in certain situations.

A good example of this three-level trophic system--trophic meaning feeding--comes to us from the Midwestern part of the United States in terrestrial systems. And there, we have wolves that exert top-down control on elks by eating them and also scaring them. It suppresses the reproduction rate. And the elks control the plant community by eating lots of saplings. And they suppress forests from coming back. Now, right now, I'd like for you to just concentrate on top-down control, the blue arrows here.

And let's look at an example from a marine system, a very similar system, and let's try to predict the dynamics that occur when we have double-negative interactions. So again, here's one example that we have from the kelp system, one of my favorite examples. Sea otters eat urchins and control their densities. Urchins at high densities control the luxuriant production you see in kelp beds. They can form fronts and kill the entire ecosystem. So there's strong top-down control in the system.

And what we had found--what do you think's going to happen when you have two negative interactions? What does that usually add up to, a positive or negative? Right. So we get a positive--and this is a facilitation. And it actually turned out to be the case. When we killed off the sea otters for their pelts 100 years ago, we saw urchin populations increase, and they decimated kelp populations. When the Endangered Species Act came into fruition, the sea otters were brought back. And summarily, as the sea otters re-colonized an area, the urchins went down in numbers, and we saw kelps recovered.

This is strong evidence for top-down control through what we call a trophic cascade; that is, two direct interactions lead to a cascading indirect effect in the system. In this case, it's facilitation. So if we take this model of top-down versus bottom-up control, let's apply it to what we know about coastal wetlands, okay?

Early studies in the 1950s and '60s went in there and said, is there top-down control in the system? They collected the grasshoppers, the snails, and they looked at what was in their guts. And they found mostly dead plant material. And they saw that the plants didn't have many bites on it. From that observational data, they concluded that grazers were inconsequential in this environment, that instead, the plants had won out on the evolutionary arms race, so we can just eliminate that box. We don't even have to worry about food webs. Let's just worry about physical factors and bottom-up control in the system.

But there's still a lot of animals. And they said they're getting their nutrition, not from eating live plants, but from eating dead ones. And we call those detritivores. And the idea about this, how organisms get the nutrition they need is that the plants are dying on their own terms. They're then infected, that dead material, by fungus and bacteria. And that's effectively a cheese and crackers, I like to call it, the cracker being the carbon from the dead plant, and the cheese being protein and fats, lipids, that increase over time as fungus and bacteria build up populations there. And those are the goodies that these grazers are waiting for at the picnic table.

So that theoretical understanding of the system or idea then gives us predictions about what happens when we find an ecosystem that's dying with lots of invertebrates. So here's--this is very common in salt marshes. We have localized die-off areas where the grasses are dying back; they're dead. And there's lots of invertebrates in the areas. And they always assume these areas were detriti-lollipops. Physical stress had come into the area. There's a lack of nutrients. The plants are dying. There's a lot of cheese and crackers, and so grazers are moving into the area.

We all know there's a difficulty in correlation and causation because you can be mixing up your independent and dependent variables. And they never tested the alternative hypothesis with experiments that grazers could be generating these areas. When I was just a little bit older than you, I went out into the salt marshes, and I saw these grazers not only eating the cheese and crackers. They're big densities, and they were grazing the grass. And they were doing it in a very unique way, not like a grasshopper. These snails I knew from high school biology had belts of teeth that come out of their mouth, like the movie Alien. And it's rows of teeth, and it comes out like this on a big stick, and it rasps away. And they can make razor-blade-like cuts in the stems right here. And what was in there, it looked like it was infected with fungus.

So based on these observations, I then asked the question, can snails that actually do graze live grass control the growth of the amount of biomass we see out there. And what is the relative effect of that top-down control in relation to adding, sprinkling more nutrients into the environment? So I got in my truck, went down to the hardware store, got some hardware cloth that has zinc on it, and the snails absolutely hate to climb on it. So it's a perfect contraption for building. But then I put cages out in the marsh. And I did a fully factorial experiment.

We have a control situation, which is normal snail abundance, 100, 200 snails per meter squared. I removed the snails with normal nitrogen. I added up resources, added resources for the plants with more nitrogen. And this is normal snail abundance. And then I took away the snails and then added nitrogen. And we got whopping effects here, both strong bottom-up and top-down effects. What we found here, this is what a marsh looks like at the end of season. And this is a marsh on snails. So marsh off snails, you can see that there's almost a 60%, 70% reduction in biomass just due to the natural course of grazing in these systems.

So it's currently under strong top-down control. And that's counter to the theory of what I read in the books. If we cross that with nitrogen, we see that nitrogen indeed will increase production. It's resource-limited. But the difference between control snails and that of removal is--now, it's a sixfold increase. And that means that the top-down effect of snails is even stronger with more nutrients. You add nutrients to the marsh, it's going to stimulate these snails to graze. And there is actually more of those grazing marks, which I'll call radulations, because their teeth, or radula, on those stems--when they were fertilized, they're likely much tastier.

So those of you who don't believe pictures, here's the data. These are the treatments of snails. This is control snails and if you remove them, and the amount of grass in that system. And orange is not fertilized, and blue is fertilized. And what you see in the not-fertilized treatments is that if you remove snails, you get a threefold increase in biomass. However, you get a much stronger effect in an interaction. The effect of snail removal depends on the presence of nitrogen. You add more resources, and the effect of removing them, boom, goes way up. Those snails were keeping those plants from attaining the high biomass that they could. Their top-down effect is stronger under nitrogen in that system.

So I presented this at scientific meetings, and scientists walked out of the room. They said, that is absolutely not happening. It must happen at night. I've never seen those snails graze that grass. There is no way that we're turning over this marsh paradigm based on this information. So what do I do? I was thinking about what could reconcile this. They never found live plant material in the snail's guts in the environment, but I'm seeing them graze this grass. But it looks like they're grazing fungus. Maybe they're farming fungus, and we agreed that's what they're after. They're just getting it in a different way, a more active way.

So I asked some of the scientists who didn't believe me, let's do experiments to test our relative ideas. So first thing we did is we went out into the marsh, and we formed this question: are snails farming fungus on salt marsh - cordgrass leaves, and does this facilitation of fungus, an infection in the plant, lead--is the mechanism by which they're controlling growth? And if that's the case, it would reconcile our two observations that seem counterintuitive.

So the first thing we did is we did a natural survey. This is observational work. And we went out to areas and sampled leaves that were unscarred and those that were scarred. And this is the amount of fungal biomass on those two types of leaves. And you can see there's a 1,500% increase in the amount of fungal biomass on leaves that have been scarred. So it looks like the snails' activity are facilitating some kind of infection in the plants. But we need to test that experimentally. We don't know if there's a causal relationship. So we did that. We had a natural condition, and then we removed snails, and then we removed snails and simulated their radulations with a little razor blade. It took a long time.

Each one of those snail cuts was simulated in those grass blades. And what we see is experimental evidence that snails do facilitate fungus. If you remove them, the fungus disappears, the scars start to heal. And this was very interesting. If you take them away, but you simulate, you get more fungal biomass. Fungal biomass is on the y-axis here. And this suggests the snails are facilitating fungus and then cropping down what happens to be their favorite food, and that environment potentially benefited from it. How do the snails--so the fungus benefited from this interaction. There's more fungus when snails are present. How does that affect the snails in turn?

So we went out there and took little baby snails because they grow faster, and we gave them these different substrates and asked them how fast they would grow if these substrates affected their growth rates. Indeed, it did. And it was proportional to how much fungus was there. This is the amount of snail growth, and these are the same treatments here. And what you see with more fungus--increasing fungus availability, we have increasing snail growth rate. They didn't die without it. But they just stopped growing very much.

So we have three species in this interaction, though. There's a host. There's a plant. How does this interaction affect the plant? Well, you have to tease it--we know that snails have a negative effect. Is the mechanism disease? You have to take that disease away. The way we do that is with ointments. So I use a fungus version of ointment, like a Neosporin. We just put a fungicide on the environment with snails. So we had 30 cages with snails, and 15 of them got fungicide. What is the effect on the plants? And it was a really amazing effect, I thought, is that both these plots have 150 snails, and after four months, when you apply fungicide, you simulate the effect of removing the snails in that environment.

So this suggests that almost all the top-down effect that snails are exerting on the system is because they're facilitating disease, and we know that's because they're farming the fungus on the leaf's surface. The snails in this environment didn't die, but they just slowed the growth over time, and they continue to graze the grass during that time period. So then let's ask the question, these snails can control grass growth through facilitation of fungal infection. They can have a big top-down effect.

What's stopping them from killing all these grasses? Well, anybody who's been out and swum in a marsh --I don't know if anybody's snorkeled in a marsh. I have. It's one of my favorite things to do. Blue crabs are all over the place. They go in there, and they're grabbing crabs; they're grabbing snails. And so an intuitive hypothesis is that potentially, these snail populations are limited by predators in the environment.

So on to the heretical hypothesis. Does a trophic cascade regulate salt marsh grasses where predators suppress high densities of snails and keep those grazers in check? And we tested the effects of predators on grazers in two different ways. We used one of my favorite techniques, tethering snails. And we looked at whether or not, in areas where we had high crab density, do you also have high predation on snails and low snail density. And then we excluded the consumer--the predators in this environment, which are primarily blue crabs, and we said, does the population of snails change over time.

So we tethered about 2,000 or 3,000 snails. This takes about four or five days sitting on the beach. You take fishing line, you have glue, you take little PVC pipes, and you make, like, clothespins. And then you have all of these snails and hope they don't tangle up their lines. You spread them all out, and then you go out in the marsh, and you go down to areas like this that are loaded with alligators, so you're looking over your shoulder looking out for alligators. And then you plug those in the marshes and areas with both high and low densities of crabs. And look what happens after a tidal cycle, or two tidal cycles, or three. And then you also put predator exclusion cages and come back, like, four or five months later.

And this is what we found with tethering. Four or five days of work, nonstop work, was destroyed by blue crabs in about four hours in these systems. This is snail mortality in high crab density areas--98% of 1,000 snails that were laid out were cracked open. These weren't snails that were picked off by fish. They were cracked open, which is a telltale sign of a blue crab. Remember, they can eat one in 15 seconds. It's amazing to see one do that. They put it in their claws, they spin it around with their mouth parts, they pick out a weak spot, they clamp down, it breaks it, and they spin it around like a corn on the cob and eat all of it. It's pretty amazing. And in low crab density areas, one snail was lost every other day.

So this suggests that--and we also found very few snails in these areas but high abundance of crabs. This suggests it's observational data that predators can control their density. If you combine that with cage exclusion results, and you keep those predators out over a five-month period, the number of snails they're recruiting, the babies come in from the water column. They land on grasses. And their survivorship goes way up, and they start growing into adults.

And so this experimentally demonstrates that predators can control the population. And if you put this together, this is the conceptual model we have. We've got to get rid of the red X. That's what I'm telling everybody in the audience. And they're like, they love the red X. We don't have to worry about the food webs. The snails are a grazer. Experimentally demonstrating that have strong top-down control and that predators control the density. And the response I got is that it only happens in the cage world. If you put too many animals in there, you're going to get overgrazing.

Is there a relationship? Is there evidence that's outside a cage? And so ecologists have to ask, does cage world equal real world. And we use other methods. And we start using correlational approaches because we have a mechanistic understanding that can give us some hypotheses. So I went to long-term data, Department of Natural Resources, monitored blue crabs, and looked at the relationship of blue crab variation, snail density variation, and the amount of marsh grass over a 15 year period. So just looking at the top of the food web, this is the variation of blue crab abundance from trawls by the Department of Natural Resources over a 15-year period. And here's snail density. And you see a negative relationship.

In years that you have more blue crabs, you have lower snails. In years with lower blue crabs, you have higher densities of snails. And in long-term monitoring plots in those same areas where we're measuring snail density, we saw a negative relationship at the lower part of the trophic level between snails and grass. As you increase the number of snails in the system, you lower the grass biomass. And this suggests that there is spatial and temporal generality of this phenomenon that we're experimentally demonstrating in these grasses. So when people started to drive by this, the alternative hypothesis, but what they said now is we believe it's growing in southeastern salt marshes. It's probably not going on elsewhere. And it's probably idiosyncratic just where those snails are distributed in Georgia and South Carolina.

What this makes us do is that we have to get rid of that red X for this region--our food web and understanding here. And things change when that happens. You get rid of the red X. The herbivore box changes. We know snails are really important. That top-down arrow becomes prominent. The amount of detritivores in the system is less than we thought because we mischaracterized this organism. And indeed, we have indirect facilitative interactions going on in this system, in this environment. But what about, is there generality? Is top-down control of marshes, like my critics are saying, just idiosyncratic? You just found it there; it's part of the natural history. Or is it a process that's common around the world?

So the past 15 years, we worked with high school students, college students around the world. They set up experiments, and they tested these ideas. And what we found was it wasn't unique to that spot. It wasn't novel. It was, in fact, very common. So we went to Argentina and Chile. We went to New Zealand, Australia, a lot in Europe, and we built a big network. And we excluded the grazers. And what we found, there was strong control of these plants by the grazer populations. Very interestingly, look at the diversity: the players were all changing in these systems, but the process was the same. And we saw--one of the most abundant organisms that we saw were crabs. And actually, we should put that here. We just found that the crabs are here in California.

So this is science that's happening right now. And it's going on, and students like you are involved. And these crabs, like the snails, facilitate fungus, so they can have a strong top-down effect in the system. So grazers are really strong in the system.

Okay, let's think about predators. We've only done this in one other system, and it's unpublished. So this is also research you could get involved in if you were interested in these other systems. Now, sea otters, it turns out, are coming into salt marshes in California. I was super-excited because when I grew up thinking about studying food webs in salt marshes, it was just about small organisms, and I had ecosystem envy. I saw the sea otter story in my textbook, and I'm like wow, that's amazing. You can have orcas and sea otters and sharks at the top. We don't have that. Oh, yeah, we do. It's just our books were wrong. And it turns out when you conserve otters, they like to hang out in salt marshes.

And the salt marshes in Elkhorn Slough, California, have been dying off, and people have attributed that, guess what, to physical factors like sediment, climate change in those environments. If you go out there and look, we checked it out. They called me and said, what do you think about the processes in the salt marsh? I said, let's look and see if you have super-abundant crabs on the creek bank, crabs stuffing plants in their mouth, eating during the daytime. And in this little pocket over here, where the otters were starting to colonize, they were eating the crabs. And the mothers were out there snorkeling, eating the crabs. It was pretty amazing.

So I said I think we should probably test for the relative effects of top-down effect in the system. So with my collaborators, we tested this hypothesis, and it's not published. It's in the process. But here's some of the data. In areas where sea otters are coming in, we see lower crab abundance. And if you exclude the sea otters, check that out. You get a lot of holes. The crab, the larvae get in there, and they start to grow up as adults, and then they start grazing down the plants. They start eating the roots. And on the creek bank, when this happens, you get a lot of erosion in those environments.

So our idea here is the expansion of sea otters in here is reestablishing a trophic cascade, suppressing grazers, and likely going to rescue this system from the erosional processes that everybody's worried about. It may not be physical processes.

So here's the data again, which data's very important. Pictures--if they speak 1,000 words, you should put those in there, too. We have sea otter exclusion and control. So exclude the otters, you get a threefold increase in crabs per trap. The number of burrows goes up. And we also see that with aboveground biomass--the amount of plant goes up significantly. And that is increased over time as well.

So if we put all this together, here are some conclusions that I'd like to make before we get to the questions. First is that top-down control by grazers and predators in coastal wetlands is an important factor. It controls the amount of plants in that system. And we know that that's linked to the amount of services that are being generated. More plants equals more fisheries production. And if you're interested in those services, we've got to incorporate food webs into the management. It's a new way of thinking about coastal wetlands. We have to redo our textbooks and redo the way we think about management. Management of blue crab populations and sea otter populations is important for the health of those ecosystems. We need to think about preserving those predators, and it may be even more important if other climate stressors are imposed on those plants. Those predators protect them from overgrazing.

Here's a more general conclusion is that from the snails, we saw snails--really small biomass. It's not intuitive that they can control a massive, extensive ecosystem that's so vast. The idea is that small guys can have big effects in these ecosystems if they're interacting with microbial disease. And we're doing surveys, and we're finding this is the case in a lot of other ecosystems. And I'll talk about that in lecture four.

And the last one is that trophic cascades occur across diverse ecosystems. Another paradigm that I was taught when I was about your age about trophic cascades is they can be very powerful, but they're very likely to happen in systems where plants are very tasty like algae-based systems. Those plant systems that are woody and that have vascular plants are not susceptible. And this shows that they are very susceptible. And those food web interactions are a critical--understanding them is a critical part in understanding what controls the pyramid, the biomass pyramid, and also conserving those systems. Thank you very much.

[Applause]

[SILLIMAN:] A question here?

[STUDENT:] What can we do to promote people to know the benefits of the marshes and the impacts that they have on society?

[SILLIMAN:] That's a very important question. So it's the job of scientists to speak--do public speaking, actually write in blogs, and write in journals--actually in newspapers. Those are things that people read. People that are managing these ecosystems and that care about the services, you don't read the journal articles that I'm producing. So there needs to be a--there's a science communication gap and there's professionals.

So working with places like the Howard Hughes Medical Institute, science communication journalism departments--we're interacting with those now at the Duke Marine Lab to get the word out. And it's also important to participate on panels, to volunteer time, and work with managers and conservationists, go to those meetings. You have to get out of the silo and not just publish in those journal articles. You have to go participate in the public discussions. Great question. Yes?

[STUDENT:] When you were talking about setting up the experiment, the crabs and the snails, you mentioned that there were alligators. And so how do the alligators affect the snail populations there and the crab populations and the grass populations?

[SILLIMAN:] That's a great question. You're thinking like a food web ecologist. The first thing I had to figure out was why are alligators there. From Discovery Channel information, they don't have salt glands, so they shouldn't be in a marine environment. And it turns out we've tracked them; we've captured over 200 of the alligators. We're looking at that question. Their guts are full of marine organisms, like 90% by weight. They eat shrimp. They have blue crabs. What they do about every six or seven days is they go rest in freshwater environments, and they dump all their salt. Amazing adaptation for an organism to live there.

So how could they--they're eating blue crabs. Could there be an effect on the trophic cascade? We've manipulated their numbers in swimming pools--a bit dangerous. But if you have the right people to do it and know what they're doing with handling alligators, you can do that. And they can. They can affect small populations in swimming pools. My idea is that they're probably not, because they don't eat that much, controlling the blue crab populations. They're likely tracking them.

However, they could scare blue crabs--blue crabs are scared to death of these gators; they smell them--up into the marsh. So what could happen is they could actually make the three-level trophic cascade instead of canceling out and suppressing blue crab effect on snails, they could amplify it because of the spatial complexity in the system. The alligators don't move into the marsh. They stay in the creeks. Great question. So we don't know. That's something you could help out. Yep, over here?

[STUDENT:] Yes, you said the snails were, like, farming fungus on the grass. How exactly does that work? Do they actively cultivate the fungus on the grass so that they can consume it?

[SILLIMAN:] Great question. And when I started to make these observations, I started to read about ant fungal farming interactions that I saw on the Discovery Channel. And they're very complex behaviors, where the ants will transfer cultivar down generations, purposely planted in areas. They will pick off competitors. They will add nutrients.

If you look at the snails--and we have in all those different ways--they don't show any of that complexity. And it turns out that fungal spores are everywhere. They're on the plant, so if you cut it with a razor blade, it gets infected. So simple mechanical opening facilitates the fungus. And I think simple positive feedbacks because they cue it on the fungus will then--they'll continue to eat that. One of the interesting things about that is that they don't home to the scars. And that doesn't make sense evolutionarily. Why, if you're going to commit to something and put an effort into it, aren't you defending it? You're not going to be helping everybody else out. Well, it turns out the more these stems are scarred, they get shorter. And it increases their predation rate. And so they show absolutely no preference to going to one or the other.

So it's characterized--in the ant world, it's characterized as this proto --it's the beginning of farming. It's simple, mechanical behavior that facilitates the growth of your favorite food. So if you just threw oranges in your backyard because you knew they would grow, that would be considered farming in this low level. And then the idea is that, in time, certain organisms, it evolves more complex. Oh, right here, sorry.

[STUDENT:] So in 2014, there was a really big die-off of aquatic life in the Pacific. It was called the Great Dying. What do you think caused that, specifically for sea otters, because a lot of otters died. They were collecting hundreds of bodies every day.

[SILLIMAN:] So the die-off of organisms in the marine environment is a mystery. I'm not familiar with the sea otter die-off. But I can tell you some of the hypotheses about sea otters disappearing has to do with either disease or predators in the environment. And one way they infer the relative importance of that is the number of sea otter bodies that turn up relative to the population drop. In Alaska, for instance, everybody saw sea otter populations dropping over time, and they thought it was disease. They only found about a handful of diseased organisms in the environment.

However, they found a lot of killer whales--rogue killer whales, three or four male killer whales that were specializing in the sea otters. And when you do mathematical models, they told us in that situation that it was actually top-down control. That can vary, depending on where you are. We need to investigate those. Up here?

[STUDENT:] I was wondering if you've ever considered chitin, the natural polymer that's really abundant in crab shells and shrimp shells. I was just wondering if you've ever considered that for the benefit to the plants in the marshes?

[SILLIMAN:] In the amount of chitin that's in the crabs and snails?

[STUDENT:] Yeah. So in previous research--

[SILLIMAN:] --nitrogen?

[STUDENT:] In previous research, chitin is beneficial to transpiration or as a natural insecticide or pesticide. So I was wondering if you've ever taken-- considered that in--

[SILLIMAN:] I have not. That's an interesting idea. There's certainly feedbacks between the organisms that are not necessarily based on feeding in those environments. So the mussels that are in the environment that form, they do some feeding. And then they're defecating in the environment. Decomposition case, if there's exoskeletons that are shedding, I have not looked and put some of the skeletons in the environment. That's actually a pretty interesting idea that you could test because the fiddler crabs are shedding their shells at a fast and abundant enough rate to actually increase the amount of chitin in the area. They have direct effects of chitin, and it also decomposes into nitrogen. That would be an interesting experiment to do, and easy enough. Cool question.

[STUDENT:] Thank you.

[STUDENT:] I was wondering if the grasses--if they're dying off from the fungal infections or from the snails eating the fungus out of them.

[SILLIMAN:] Well, both of them have to be there. And it turns out if you use the experiments, the snails, the main mechanism is that they open up the wounds, and then the fungus gets in there, and the plants shift from a growth metabolism to a wound metabolism. And they continue-- that dead plant material is being generated, and the snails graze that, and then it reduces biomass over time. So it's a combination effect. The fungus is incredibly important for that question. Okay.

[STUDENT:] After coming to your conclusions, would you consider the effects of top-down forces to be greater than bottom-up forces?

[SILLIMAN:] I think both of those are important in the system. If you remove bottom-up forces from the system, you won't have plants. So you do need nutrients for it to grow. And I think they're both very, very strong. And their relative effects can change, depending on the consumers in the system and the amount of nutrients. So we can't ignore either one or the other. We have to investigate both.

[Applause]

[Music plays]