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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 first lecture is titled "Trophic Cascades in Rivers." And now, Dr. Mary Power.

[Applause]

[POWER:] Thank you. So thanks so much for the Howard Hughes Medical Institute folks for inviting us to talk about ecology today. And the kind of ecology that we'll focus on is one that I'm particularly passionate about, food web ecology.

Ecology simply is the scientific study of how organisms interact with their environments. But these interactions are never--almost never--simple and direct. They're almost always mediated through a web of indirect effects and other organisms and other factors that you may not be thinking about at the moment. So there's this complexity. And when we focus on the job that this little bug, this mayfly insect, an aquatic insect, has, it needs to go into this world, find enough to eat itself without becoming prey. It has to eat and not be eaten. This is a big problem when you're in a dangerous, heterogeneous, changing world.

So how do they do it, and how do we think about this and try to make predictions about whether the mayfly will be safe or the fish will get fed? We think about food webs. And this would be a characterization of how energy and nutrients flow up from the producers, the plants and the microscopic algae and seaweeds that fix carbon into edible forms by using sunlight energy. And then that's grazed by the herbivores. And the herbivores are eaten by predators. And some predators eat other predators.

So here, you have a depiction, kind of a road map, of how energy and nutrients are flowing up through a web of connections. And we call these things trophic levels, the predators, the herbivores, the producers. Trophic is just a Greek word that means "feeding." So they depict that, but they also depict something else, something rather different. And that is whether any of those predators can actually reduce the abundance of their prey, whether they can control populations. So can that heron really suppress the populations of the minnow or the steelhead fish there? Or if they were in abundance, could they suppress the insects? Or could the insects suppress the blooms of the algae?

So we'll talk about that. And these are top-down effects. And if you find these chains through the complex web, you find some chains that are really strong and do mediate these chains of predators that can actually even ultimately affect plant abundance by their effects on their own prey, the prey's prey.

So you find these top-down controls. And that's what we call trophic cascade, if that happens. So we're interested in that. Now, it's very natural for all of us to think, for example, where the world is green with a nice forest in Michigan or where it's more barren looking in dry prairies of Kansas, the first thing

we think of: oh, it's got to be climate that the plants have more water, so we can grow forests in Michigan, and Kansas not so much. But it isn't necessarily what's controlling the vegetation. The thing that's hidden is the possibility that predators may be involved. And Michigan ecologists actually looked out their window. It looked green. So they said, well, maybe the world is green because predators are suppressing herbivores, the yellow circle. And herbivores then cannot suppress plants, so the predators are indirectly protecting the plants. So that would be a trophic cascade with three trophic levels. Now, a Kansas ecologist, Fretwell, looked out of his window, and it didn't look all that green in Kansas. So he said, well, maybe the world doesn't have to have three levels. What if it had fewer or more?

So what he reasoned was an extension of this idea that, if plants were alone in the world, one trophic level, they would probably grow up to an abundance where they eventually became limited by their own resource: water, nutrients, maybe sunlight. But if you added grazers, the plants would be suppressed. And they wouldn't be resource limited anymore. They'd be grazer limited. And the grazers would be resource limited. They'd run out of plant food. But then you could add predators. You'd get the Michigan situation, where the predators are protecting the plants and suppressing the grazers. And there can be important predators of predators. You'll hear about some in my talk.

So you can get a situation where you have four trophic levels or maybe five, maybe even six sometimes. But there's a generalization that comes out of this idea. And that is that, if the world has odd numbers of trophic levels--one, three, five--it should look green. We should have vegetation released. And if it has even numbers, it would be barren, with two or four, with the grazers released to suppress the vegetation. And what happens to the vegetation is what happens to the world. Often, vegetation structures the way we look and feel and can move through the world. It's huge. So a lot of the targets of this trophic cascade ecology involve trying to predict what is going to be the impact on plant biomass.

So are some of you skeptical scientists or scientists-to-be, already thinking about what's wrong with this really simple, cartoonish idea? I see it. I see it. Good. Okay, so there are things wrong. Plants--green doesn't mean edible. So that means that, if we see a forest, it's a one trophic level system because the plants figured out how to be toxic or spiny or just not nutritious enough. Now, also, how do you count trophic levels when you have things like frogs that are very impolite, and they hop from one trophic level to another? They're herbivores as babies, and then they grow and eat insects, and they're predators as adults. And we--and rats, and lots of other common species--are also very omnivorous. So that's a problem. Then, if you're out there in the real world, you might be both hungry and afraid, and you're making trade-off decisions.

Prey populations are often co-limited by fear and hunger. And those factors interact. You might make different decisions about foraging. So how can we say that the one population is always resource-limited, and another population's always consumer-limited? So there are all these problems, and then there's a big problem that what limits life on Earth isn't always trophic. It isn't always getting enough food or being afraid of being eaten.

We have other factors that can kill and change distributions. So you'd think with all of this going on in the real world, this theory would never work. But in my experience, it's been really useful. It's been really useful underwater to think about this model and try to understand then why is the world looking green, barren. Why are populations thriving or not thriving?

So let me tell you why I like working in rivers. Rivers, for one thing, are very convenient for experimental and comparative work because nature has offered you a string of beads where the beads might be replicated pool habitats that are connected by shallow riffles. So the dark blue in the drawing here are the deeper pools, habitats for bigger organisms. The riffles between are shallow and faster. And little organisms, or maybe the juveniles, would be there, but it would be dangerous for adults to be there for reasons I'll tell about later. You can imagine that they're victimized by terrestrial or bird predators. So that's one advantage in rivers.

And another advantage is that life is miniaturized there. My father actually helped me build my first experimental stream enclosure here in Panama. And dad and I put that fence in, and there's a herd of armored catfish that you'll meet shortly grazing there. So I can keep track of what they're doing. And what they're grazing is also miniaturized. In that drawing, it's what you would perceive macroscopically as slime on a rock. But if you scrape it up and look under a microscope, it's a very diverse and beautiful world. And often, it's thinner than the thickness of your hair. It's that little skin of life, but it's very, very interesting life, algae.

Okay, so we're going to talk about two extremely different rivers and two extremely different grazers, grazing fish. Both eat algae. This first talk is going to emphasize how the traits of these grazers are making a difference in the length of food chains through food webs. So we'll start in Panama, where that big lumbering armored catfish is grazing. So here's the Rio Frijoles, Bean River, of central Panama. And you're walking down this river. You come to the shallow riffle where the water's wrinkled and sparkly. And then you come to the deeper, quiet pool beyond. Then beyond, you can see the next riffle. And then there's another pool. And this would be in a sunny reach where the river has kept a floodplain open.

But you can also go to places where the rock is harder and the forest can grow right up to the edge of the river and shade the pools very darkly. So this repeated pool-riffle sequence gives me a chance to compare what's going on in sunny pools and dark pools, which probably makes some sort of difference. You don't necessarily know what when you're first exploring. But it probably matters somehow to these grazing armored catfish and the algae which is their food. So here they are. There were four species. Because they had armor, I could use just surgical wire and moccasin beads to mark them as individuals.

I followed 1,300 fish for three years in my life with catfish. The most common is the black species. And it's called in the aquarium trade the bristlenose catfish. In deeper pools, this guy is absolutely safe because it's outgrown all the gape-limited predators. In the foreground, you can see there's a characin fish. This is the same family that gives us piranhas. And even these little guys are active predators. They'll eat animals they can fit in their mouths. But they can't fit that big old armored catfish into their mouth.

Now, what are the catfish doing with their mouths? Well, they're making kind of a seal over flat substrates with those suckorial discs, and they're using four comb-like tooth plates to scrape the algae off. These armored catfish--how many of you have seen them before? People keep them in aquaria to keep the glass clean of algae. So they're very useful in aquaria. But what they're doing in nature is about the same thing. They're scraping algae off of flat surfaces. That makes it easier for an ecologist to know how much food is available to them day by day in their habitats. You can measure the area they can graze. You can measure the growth rate of algae on small parts of that area and extrapolate. And you've got how much food is renewing for a fish in a pool at a given time.

And I just want to introduce you--you'll hear a lot more about algae in the third lecture--to how cool it is. These are algae that grow on microscopic surfaces. That surface in the scanning electron micrograph, the right-hand side at the top, it's growing on a surface that is the diameter of your human hair, okay?

So that's what you have if you're an alga, and you're getting grown upon. But those cells are really high-quality, nutritious food, and they grow very fast. That's important. But you can't really see anything but a thin, barely slippery skin if you and the armored catfish are competing for finding algae, because they'll win. So what you do is an experiment, very simple. But you just lift natural rocks or artificial tiles with the rock-like surface up where the catfish can't get them. And then you can measure how fast the algae grow when they're not grazed in sunny and dark pools. And no surprise to those of you who know plants, the algae are growing a lot faster in the sunny pools. Those are the orange-lined two pools.

What I'm showing here is days and the 16 days total. Over the first four days, the growth is really fast, and then it's starting to level off. So I look at the first four days because the catfish don't give them time to level off in their growth. And that's the standing crop or the abundance of algae that you'd measure just by taking a scrape. So it's like a snapshot of abundance, the mass per unit area. So you can see that is growing faster in the two pools that are sunny than in the purple lines, which show results from the two shaded pools.

Now, the catfish are also more abundant in the sunny pools. This is the months of the year going from September to August. And here is the density, the number of individual catfish per square meter. So what we have in orange here are averages from about four sunny pools that I tracked them over a year. And what's this big change in density doing? You know, this is a bit counterintuitive for those of us who live on earth, where the area of our environment doesn't change like this.

But in rivers, rivers expand when the rains come, and they contract when the river dries out in the dry season. So all we're seeing here is the beginning of the dry season. And the density's getting higher because the catfish have less and less area. But then the rains come, and they can expand out. And so that's what's happening in the rainy season. So we see the catfish are tracking growth rate because they're a lot denser always in the sunny pools than in the dark pools.

And those were data I got by getting on my mask and snorkel and snorkeling through all those pools with an underwater flashlight so I can look under the ledges. When I got in, a lot of the catfish were scared under the rocks, but I could find them. I could see to the end of their little cavern refuges and just count them. So that worked well. But still, I didn't know if my snorkel counts were giving me information about where the fish were actually feeding, or if they just hung out in those pools, maybe hid from me there, and then grazed elsewhere.

So if you want to really know what's going on with their food renewal and their tracking or their feeding on it, you need to actually make direct observations of the fish in nature. So I watched two dark and two sunny pools, just sitting on the river bank for actually day and night, for days and days, because the fish are active day and night--at night, I use dim underwater flashlights under water--and kept count of--here are some of my little marked armored catfish. So I would--every 15 minutes, I'd count the number of catfish out on this platform, which I'd gridded with little markers beforehand. And then between what we call those scan samples where I got counts of how many fish were using the platform, I'd watch individual fishes of various species and sizes, keeping track by mapping it, of how much grazing area they covered.

So that little guy, maybe in my five-minute observation, had covered this pink area. So I can interpolate from this 25-by-25 centimeter grid how much area it grazed on its own in that time. So I got two kinds of information: counts of all the fish and grazing rates for individual fish. And those two pieces of information let me compute how long it will be before any fish gets back to regaze a small site on that substrate.

So this may be not totally intuitive. But if you want to make that estimate of the grazing pressure on the algae or the return time of any fish to graze that small site again, then that time is equal to the area that they're sharing together, over the number of individuals that are using that area collectively times the area that an individual can graze per time. And if you just cancel area with area, individuals with individuals, you see that you get one over one over time on the right-hand side, which is equal to return time of the fish to a site on the left-hand side.

So why do I care about this? Return time is also the time the algae had to grow between grazing bouts, on average. So that's why it's important, because you can tell how much food is going to be at that small site when they come back if you know how fast the algae is growing and how long it had to grow before it got grazed again. So the return times in these pools with the dense populations of armored catfish are on the order of just half a day. That's not much time for growth. Very intensely grazed. And in the darker pools, they have between one and five days to graze, so a lot longer.

But the algae are growing a lot faster in the sunny pools than in the dark pools. So the growth rates of the algae here are on the order of five or six or sometimes even ten times greater than the growth rates in the dark pools. So multiply the rate at which algae can grow--mass per time--times time, and you get the mass --the algal standing crop that should be on that site when it's about to be regrazed.

This is the predicted algal biomass that should be at those sites in the sunny pools and in the dark pools. And the important thing to notice with these four numbers is that the estimates for the dark

pools bracket the values for all the pools. So that suggests that the catfish are evening out the effects of more sun, which does let algae grow faster. But it gets grazed faster. So the catfish are grazing it more intensely, and that dampens out the effect of that added fast growth on the accumulation of algal biomass.

So that's kind of interesting. And one can check that directly. These algal standing crops were really thin. They're barely slippery. So I had to take my Swiss Army knife out, flake off bedrock, take it under the microscope, boil off some of the algae with acid, and count it. But that did the trick because I could see that the abundance of algae on the sunny pool substrates was about the same as the directly measured abundance of algae in the dark pools, which tests this prediction from the model. So that's what we've got.

Here's a summary just of what I saw. This is actually averaged over 12 months and 16 pools that range in canopy from very dark, with just a 2% or 3% open sky through the forest canopy over the pool, to very sunny, where most of the sky over the river would be open. So that's the sunny pool.

So yes, algae are growing faster. Productivity is higher in the sunny pools. The catfish density is tracking that, denser in the sunny pools. The algal biomass, the measured algal biomass, is the same in dark, half-shaded, and sunny pools. And so, then, is the growth rate of these catfish.

So the guys in the dark pool are growing just as fast as the guys in the sunny pool, even though their food is growing more slowly, but they're not dealing with the crowds. So this is what leads to the support for a very useful, very simple theory called the ideal free distribution. You don't normally think about catfish as being ideal and free. But now, you really should. Because ideal means they are smart enough to make really informed decisions about which pool is the best for me at any time. They've got to know what the range of algal availability is in dark but uncrowded pools or sunny, productive, but crowded pools.

And they have to make a decision: would I be better off joining the crowd, or would I be better off going to a more sparsely populated, darker pool because it's not as crowded, and there might be leftover food there. So they're ideal because they're smart. And also, they're free. They can choose the best pool available in the whole 3 kilometers with 30 pools. They can choose the best at any time to make the most food available to them.

So that is not always a common situation because if there were a bully catfish or a bully any other kind of fish in a pool, they might not be able to join. But because they're big, armored, and spiny, and tough, they can have their way. They can go where they want. And also, they might not be able to get through riffles. But they do, when they're motivated to track this food. So this is what we see from pool to pool to pool to pool.

Now, we're going to see a problem for these fish on a different spatial scale, which is when you go from the deep parts of the pool up towards the water's edge along a depth gradient. Suddenly, they're not so free anymore. So why is that? And here's the water's edge. Here's heavily grazed substrate, where it's deeper. This green line happens right about at the 20 centimeter--it's about that deep--

contour. The 20 centimeter contour, you start seeing a bathtub ring of algae in many places--Panama and other places grazing fish are common. And it's because something is keeping those grazers out of the shallow water, even when they're really hungry in the deeper water.

So what's inhibiting them? Predation. These catfish can outgrow all of the swimming predators because swimming predators are gape-limited. They can only eat what they can fit into their mouths in general. But the aerial and terrestrial predators have claws and fangs, and they can tear their prey apart. So they have no problem taking an armored catfish and catching it here and then ripping through that armor, getting to the soft unarmored belly, and eating the poor catfish.

So these catfish are really conservative about their safety, and they let that algae go, even when they're starving here. The time, of course, that they get it is when the river rises in the rainy season. Suddenly, it's safe enough, but only for a while.

So that's what the situation is. You can go into many places of nature, in the natural world, and put your finger on a point in the landscape where the food web changes length. That's what we're seeing here. What we're seeing is a two-trophic-level world that's barren in the deeper water. Put your finger on where the bathtub ring begins, that's a three-trophic-level world in the shallows.

Now, let's look at a very different fish in Oklahoma, the grazing minnow called the stoneroller, *Camptostoma*. And look how different it is than those armored catfish. This fish, unfortunately for it, is thin and soft, and it remains vulnerable to predators throughout its life. Now, it's a very common fish. Despite being so vulnerable, it's really common throughout our Midwest. And I studied it in south central Oklahoma, right on the Texas border.

So here's Brier Creek, where I spent three years. Brier Creek has these sunny pools that go through long, shallow riffles to get to the next pool upstream. And so again, it's this pool, riffle, pool, riffle replicated habitat. And some of these pools walking along Brier Creek were very barren. But others were filled with green algae. They were extremely striking in their algal abundance.

So I'd studied Panama before, so I wasn't used to seeing this algal contrast pool to pool, when the pools seemed otherwise kind of similar. But the barren pools had schools of the grazing minnow, *Camptostoma*. And the green pools lacked the minnows entirely and had their predators, which were spotted, and large-mouth bass.

Well, we mapped a length of 14 pools--pool, riffle, pool, riffle--and kept track of whether the pool was green with bass or barren with minnows or whether it had both bass and minnows in it. And the first time we did this, in November, there was just one pool where the two species overlapped. It happened to have a wide, shallow tail, where the minnows could get a little bit of cover from the bass. Then we did it again, and we kept seeing this pattern repeat date after date that the minnows really didn't overlap with bass in very many of those 14 pools until we got a flood. And then the flood rearranged the fish in this river. And we got four overlaps. But those sorted themselves out one way or another.

So here's a pool of minnows turning into a bass pool. And so the pattern was reestablished until the next flood--a lot of overlap, and then it was reestablished. So at the scale of the reach, there's this striking--we call it complementarity. If there are bass, there's green algae, no minnows; minnows, barren, no algae. So you're probably starting to think, I hope, trophic cascades. But let's see what happens when we rearrange the fish ourselves instead of just letting floods do it.

So we took a green bass pool, we got rid of all the bass, and we split that pool down the middle, and we added minnows just to one side. Here's what it looked like five weeks later. The side to which we added the minnows is this side on the lower part of the screen that's grazed barren here. That's just barren Oklahoma limestone and silt. And here's the green algae that is actually in what we call a one trophic level system, because we took the bass out, but the algae now are free to graze because they don't have the grazers.

So here are the data from that. We are going from 10th of September through mid-October here in time. And the average algal height is a quick and fairly decent way to measure algal standing crop if you want to do it quickly. You just throw transects across the stream, measure the height of the algae, then you have a relationship you've developed between algal height and algal weight. And you can use that in a number of ways to estimate algae quickly in nature. The algae started out high on the side to which we added the minnows in that green pool. But they grazed it down to a fairly barren state within weeks. And the side that lacked the minnows actually bloomed. We got growth of algae here because we had a rain in late September that stirred up nutrients.

So in a one-trophic-level system, the plants can respond to their nutrients. But in a two-trophic-level system, that pulse of enrichment just goes to the fish. The plants don't see it in their biomass, although they do grow faster. Okay, so that's what's going on. And then this purple line is a control pool, where there was a naturally occurring school of *Campostoma*, the minnow. And we just followed it. And they could also suppress algae against that little pulse from the rainstorm, that little pulse of nutrients.

Now, the other experiment obviously is to throw a bass into a minnow pool and see what happens. And we did that in a barren pool. We just threw one bass in. And minnows--I wanted you to see the difference between what happened to algae--again, algal height--against the same timeline. But here are shallow records that were collected from less than 20 centimeters. Remember, that's the threshold for the bathtub ring. And here are records of the algal height from deeper areas.

So what happened was when the bass was first introduced, the minnows moved into the shallows. They had avoided them somewhat before, so the algae was higher. But they got that algae while they were worrying about the bass. They were eating nervously, I guess. And then the algae in both shallow and deep substrates was released because the minnows disappeared pretty fast. And here's that same school of minnows that we didn't manipulate but just followed as a control to see how algae changed when we didn't do anything.

Okay, so you can turn the barren world into a green world, again within weeks, by adding a predator. But what's that predator doing? Is it turning green because the bass eats up all the minnows? Or is there something the minnows can do about the situation? There is predator avoidance. And to

estimate how important that was, before we did these experiments, I fenced off the downstream and upstream riffles to see how many minnows were eaten and how many tried to escape to get to a safer world beyond the bass pool. And here they are. They're milling against this upstream fence wishing they could get out, and they did eventually. We lifted the fence, but not before we counted them. So we know that it was 74 initial minnows, 40 escaped, and 34 were eaten.

So here's a simple trophic cascade. Despite all those complexities that we talked about, it does seem to work in these systems. So you have *Campostoma* when it's not inhibited by predators, can mow down algae, a barren world for two levels. If the bass are protecting the algae, it's a green world, and you don't see the *Campostoma*.

So we've talked about two very different grazers, and it's their traits here that make the difference, a really striking difference. It's even more surprising because the Panamanian stream was really contrasting in how fast the algae could grow because it went through open, sunny areas and very darkly forested areas where the jungle canopy was pretty thick. Nevertheless, the algae looked uniformly scant throughout that, and it's because this is a grazer that has figured out how to be ideal and free, not get eaten, it's not threatened by predators as long as it stays deep enough.

Now, in the Brier Creek, the Oklahoma stream was uniformly sunny, very productive. Yet the standing crops of algae, their abundance, were strikingly different in green and barren pools. And it's because this poor, thin, soft fish is not free to go eat in a bass pool, much as it would like to. So that's what sets up a three-trophic-level cascade that is very similar to other cascades you can read about in terrestrial and especially marine systems.

So that's what we have come up with with finding a simple idea that actually is very useful under the river's surface. And now, I want to just quickly go through why it might just be useful at a larger context to society. I think you can make an argument about trophic cascades influencing what we can get out of our fresh waters in general. And the argument is simplistic, but it's a useful starting point for thinking about it. It runs like this. We want clean water. We want safe drinking water, clear water often, and we also really enjoy watching predators and wildlife and catching big fish. Okay, that's kind of a given.

Now, we talked about these food webs, but we never talked about where the biomass was concentrated in the food webs. And we know as terrestrial organisms, we're kind of used to having the forest plant material really have most of the biomass. And we animals are little bit small compared to that. Here's the terrestrial system with a lot of maybe forest or even grasslands, fewer buffalo, and fewer wolves, right? But that's terrestrial. And what can happen underwater is you can have the opposite situation. Literally, in that lake I showed you, Clearwater Lake, you would go to the rocks. They'd be barely slippery. So a little bit of algae here. Thin, thin film of algae is supporting somehow a higher biomass of grazing insects. And that's supporting even higher biomass, sometimes of great big fish.

So how can that be? It works this way, that the algae are thin, but very, very productive, growing really fast. So that little thin skin is growing like gangbusters. And also, many algae, like these diatoms, are

really nutritious, as I was saying. They're excellent food. So they can support the growth of insects--even the insects can be more abundant than the algae. These insects are reproducing maybe every few weeks. So they can store some of that energy in their longer-lived bodies. And the fish are reproducing maybe every couple of years. So they're even longer-lived. So you start getting all of this energy sustaining and stored in big, long-lived predators. And if you understand these rates, you can start to understand what's not easy to understand, how a trophic biomass pyramid can rest on its pointy little head, be inverted. Interesting, huh?

Now, we're getting services from this trophic pyramid as well that have to do with the clean water. The fish suppress the bugs. The bugs suppress the algae. And the algae don't grow up and make the pool green. So that's a good thing, too. So we're getting two great services from natural fresh waters in healthy ecosystems. But what are we often seeing? I bet some of you have seen this or been excluded from your favorite swimming pools because of harmful algal blooms. It's happening, I think, in almost every state, maybe not Alaska. But this is an all-too-common situation. This is a sample of water that was just dipped up from a lake in the Bay Area of California. And this is what we call a very harmful algal bloom--not much animal life can live here because the algae at night will suck all the oxygen out of the water. And some of these algae are toxic, unfortunately.

So we'll talk about that more in lecture 3. But this is what we call in freshwater a very bottom-heavy trophic pyramid, where almost all the biomass is in algae. And I can make an argument to you that this all depends on how long the food chains can be. So if we do a thought experiment--this is simplistic again, but do an armchair tour with me as we go to a city like Phoenix, Arizona, where we basically can say we have zero trophic levels in the watersheds. The streams are all dry. And the watersheds have been overgrazed, and it's arid, so there's no terrestrial vegetation that's really grown back.

So there's a lot of smog in Phoenix, and they've had to shut down water wells on the outskirts in those arid watersheds because the residents are drinking a toxic level of nitrates in their well water. Nitrate is something that, along with a lot of other stuff, can rain down from smog. And at high levels, it can interfere with babies' respiration, so you get what you call blue baby syndrome if you have too-high levels of nitrates in the wells. And this is happening in water wells in areas like this. So that's zero trophic level, no plants to take up the algae. If we had plants, it would be better because the plants use nitrate as a nutrient. So they take it and use it to assimilate plant tissue, which is not usually toxic. And that's better. But if you have too many plants, you have that eutrophic mess that we talked about with the green pools.

So you might want insects, aquatic insects to graze that algae. But there might be too many insects. And a lot of these aquatic insects emerge into clouds, and sometimes, these clouds are doing things to us that we don't like. So you might want fish that would eat the insects. That would be a three-level web, three trophic levels. And we'd be even happier if we had four trophic levels. And we'd be even happier if we had five trophic levels, as this famous ecologist, Jim Estes, who studied the sea otter trophic cascade. So he's enjoying products of a freshwater ecosystem that made it out to the ocean. And these--you can make this argument that, if we can keep the food chains long, we can keep aquatic ecosystems healthy.

And how do we do that? Well, that's the subject really of my third lecture. We really need to think about our watersheds to keep these ecosystems in a state where we can support the great top predators that, through trophic cascades, can suppress lower trophic levels that can otherwise be problems for us. Thank you.

[Applause]

[POWER:] So I'd love to hear questions. Yes?

[STUDENT:] So when you have the bass in the pools, and you don't really have any minnows left, what do the bass eat?

[POWER:] Did you note--if you go back and look at the slide, look how hollow his belly is. He's a very hungry bass. So there are other fish, and some of them are a little harder for the bass to eat, so they last longer, like sunfish are deep-bodied and have a spine. So there are prey, but those bass are really hungry, and they're really ready to get at those minnows when they get rearranged. I think the reason they can hold on is the floods do rearrange them. Also, something about fish: they can starve a long time without dying. They can stay in the game. They just really shrink down, and that's how they make it. They can make their living on pulses that they get occasionally, more than we could. Yeah, did you have a question?

[STUDENT:] I wanted to know what can we do to sustain clean water for us to do our basic, everyday needs like showering and drinking?

[POWER:] Well, I--this is going to be a topic for the third lecture. I won't address all of those questions for all of the society. But the main thing is, think about what we're adding to these aquatic ecosystems and what we're taking out.

So in general, we are taking out water for our use. We have to be very vigilant about what we've taken and what remains and what's necessary. But we've taken water out. We sometimes take fish or big gravel materials for construction out. That changes the stream. And then we add heat. How do we add heat? We are taking forests away. We're warming the earth. Taking water away will make the shallower water warmer. That's important. We're adding fine sediments. We're adding strange chemicals. So if we can just control the sources that we're responsible for in the watersheds and figure out our extraction.

And you'll see in California, my work is under the influence of marijuana. We're trying to grapple with the issue that marijuana gets thirsty just when the river needs the water most. But there are ways to do that by storing water at other times. So we can think about timing and what we're taking and what we're putting out. And it's a very big question. I'd love to talk with you at more length and hear your ideas.

[STUDENT:] Thank you.

[POWER:] Yeah. Yes, in the back. In the gray sweater, yeah. Gray jacket.

[STUDENT:] I was wondering how long it would normally take a bass to eat, like, 30 or so of the minnows.

[POWER:] That's an interesting question. But when we've done aquarium studies, and you can see a bass with five minnows poking out of its mouth, kind of looking like a tycoon with five cigars. It was so funny. So they are voracious fish. This is also a little counterintuitive. A fish can often eat a prey that's half its own length--just gets it in, swallows it, pushes it through. And so these piscivorous fish could make short work of that. And I think we are seeing on the order of probably under two weeks, it could finish off all those minnows. Yes?

[STUDENT:] I had a question about your bass and minnow experiment. So when you split the pool so that it was one side of bass and then one side of minnows, and then I remember you talked about how they weren't eating at all. Do you think that that affected your results when you mixed them together because of how starving they were? Or would that pattern be prevalent in natural ecosystems as well?

[POWER:] Well, when we split the pool, we actually took the bass out. The bass had been keeping the pool green, but there weren't any bass when we added the minnows. So it was basically we took the bass out, added minnows to one side, didn't put bass back in the green side. So it went from three trophic levels to one trophic level. But that's still green. But in the pool where we did add the bass, and it started out two trophic levels. We added the third. And that's where his question is relevant about how fast could they have eaten those minnows up. And the answer's really fast. Yes?

[STUDENT:] You had mentioned the concept of nitrates, nitrates being put into the river ecosystems. If you added algae or any sort of plant introduced to take care of the nitrates, then how long do you think would it take for that ecosystem to stabilize?

[POWER:] Oh. I'm not even sure you could call it stable, to be honest, because you'd get the algae taking up those nitrates. They'd bloom, and then they'd be limited by something else. Maybe they'd shade themselves, and they'd probably collapse and rot, and there would be cycles. But I'm not sure they'd get to what we'd think of as an equilibrium state. Sometimes, you do see equilibrium, and they can be short-term or long-term. But it's a very important question. Also, when something accumulates in nature, often something else figures out how to eat it. And even if the algae are toxic to animals, they have their own enemies, the viruses, the phage might attack and kill. So great big algal blooms, not the world's most stable ecosystem.

[Applause]

[Music plays]