MITOCW | mit12_742f06_ses14.mp4

SCOTT DONEY: There were some questions on-- we had finished up on Thursday. We were talking about Sverdrup's critical depth hypothesis and light. And I gather from the recitation that there were some questions on that. So I wanted to go through it a little bit more to give you guys a little bit more background on that to help you with the problem set.

And so the assumptions we're going to make is that there's some mixed layer-- so this would be depth. There's some mixed layer that's being turbulently mixed. And then below that if this was temperature, it would drop off like that.

And that within that mixed layer, you have a phytoplankton community and also some heterotrophic activity. And the question was, as the mixed layer starts to shoal and shallow in the spring, at what point can the phytoplankton really bloom? At what point does the light limitation that's been holding them back all winter get relieved and you start to see the classic spring bloom that's a very common occurrence, for example, in the North Atlantic.

So there were a couple of simple equations. We were going to assume that primary production is going to be proportional to irradiance so that everywhere within this mixed layer there would be some phytoplankton. And at any instance in time they're going to be seeing an instantaneous light and that the photosynthesis rate at that depth would be some constant of proportionality, alpha, this initial slope, times an irradiance.

Now, eventually, this would saturate and turn over. But we're going to assume we're on the linear part of the curve. The second assumption that we're going to make is that the irradiance at any depth is simply going to be a surface irradiance times an exponential function, where k is our attenuation coefficient. So k equals attenuation.

Now, if you look at this equation, what units does k have to have if it's up in an exponential like that, where it's e equals minus kz? [INAUDIBLE]

AUDIENCE: 1 over meters.

SCOTT DONEY: Has to have one over meters, right? It has to have 1 over length. Because otherwise, there would be a dimension up here. And then you can't take the exponential of a dimension. So k is going to have units of 1 over meters. We're also going to assume that respiration at any depth is going to be a constant. And we'll just call it r0 because it's constant through the mixed layer. Is everybody with me so far?

OK. So then we're going to say we want to find the depth, the critical depth where-- and we'll call this zcr-- where the integrated respiration just equals the integrated production.

And that's going to be the depth where we're going to say when mixed layer is greater than critical depth, it's light limited, and you get no bloom. And when mixed layer is less than that depth, you get a bloom.

So if you go ahead and do the math, the integral on the lefthand side is just r0 zcr. We're going to integrate from the surface down to this critical depth. And since r is constant, it just turns out to be that.

The other side, we're going to integrate-- we'll plug in alpha i0 e to the minus kz dz.

And if you work this out, you'll get a nonlinear equation where k [? zcr ?] 1 minus e minus k [? zcr ?] equals r0 over alpha i0 or r0 over p0, where we're just going to set p0 to find p0 is equal alpha i0.

So if you know your surface irradiance and your respiration, you can go ahead and calculate the critical depth.

AUDIENCE: One more question on that-- just to clarify, the k par that you give, you told me yesterday that surface chlorophyll is what you plug in there. You don't have to plug in different chlorophyll [INAUDIBLE] ?

SCOTT DONEY: Right. The assumption is that the mixed layer is well mixed. And for most situations, that's a pretty good approximation. If you actually have a turbulent mixed layer, the phytoplankton concentration just can't fight it. It can't grow fast enough. The turnover time is fast enough it maintains a homogeneous layer. OK?

OK. Oops. On we go. Does everybody have that? So what we were going to do today was-- we did light. Now we want to look at-- nutrients is the next one.

And typically, the way nutrient limitation is formulated is in terms-- of you'll hear it sometimes called a Monod curve, Michaelis-Menten from enzyme kinetics. It's essentially just a curve that saturates as you get to high nutrients.

So if you have some uptake of a nutrient plotted against the nutrient, it's going to look something like this. There's going to be a period where it's fairly linear. And then it's going to saturate to some maximum value. So when you don't have a lot of the nutrient, it's going to slow the uptake down and slow growth down. But if you have the nutrient in abundance, it'll just saturate, and they'll be happy and fine, and they won't care if you add more nutrient.

The typical form of this is that uptake is parameterized as some maximum uptake. So that would be this v max times n over n plus kn, where kn is a half saturation.

And if you think about it, if n is equal to kn, the denominator is going to have a value of 2/1. And so kn really is the value of n at which uptake is 1/2 v max. So this would be kn, and this would be one half v max.

Now, there's lots of nutrients that we worry about. So, for example, the standard macronutrients are nitrogen, phosphorus, silicon for diatoms. But there's now tremendous interest in various trace metals, so iron, cobalt, zinc, perhaps some vitamins, a vitamin just being some organic compound that the particular species you're looking at can't manufacture.

So it needs to either get it from heterotrophy, or it needs to get it from the environment by taking up some dissolved organic compound. You need to worry about things like weather. For example, for nitrogen, is it in the form of nitrate or ammonia? It could be in the form of urea. It could be in the form of some other dissolved organic nitrogen compound.

And you're going to have different uptake curves and different behavior depending upon which nutrient you're talking about. And in fact, some-- and we'll talk about this either today or Thursday-- organisms don't use nitrate, a organic form that has-- the organic nitrogen usually looks a lot more like ammonia, in terms of its redox state.

And there are organisms that are not capable of assimilating nitrate. And so you need to know not only which nutrients are there but whether the organisms you're interested in can actually use that particular form of that nutrient. So it's not just enough to know whether there's an inorganic nitrogen, but what form it's actually in.

And, in fact, in some communities, there's inhibition. When you have ammonia, ammonia is much easier to use than nitrate. And if you add ammonia to the system, you'll actually reduce the nitrate uptake because the organisms will switch because they don't have to expend the energy of reducing nitrate.

A lot of interest now in dissolved organic nutrients, so DON, also DOP. The problem is that those are very heterogeneous pools. And you have to be very careful that you understand what exactly is being taken up by the organisms. You can't just call it a generic DON or a DOP. You really have to start characterizing which compounds within that are being taken up.

Typically, we don't think of DIC as being a limiting nutrient. But it can be for some organisms in some environments. And the reason why is that many organisms can only take up dissolved CO2 gas. Remember, most of H2CO3 star is actually CO2 gas.

And the rubisco enzyme, which is the main enzyme for CO2 incorporation into the organic matter as part of the photosynthetic pathway, uses CO2 gas. So if you were to look at a plot of CO2 gas-- this is now dissolved in the water.

So gas dissolved in the water-- versus photosynthesis rate, we're currently somewhere around 10 micromoles per kilogram. That would be a surface saturation value. There are some phytoplankton that would have a curve that look like that, which would suggest that they are actually sensitive to the DIC concentration or, more importantly, the CO2 gas concentration. So you'd need to know DIC and alkalinity or DIC and pH to figure out what the actual partitioning is.

So, for example, a E. hux, which is a coccolithophore, appears to have a shape like that. Other organisms-- and this is--

AUDIENCE: So this is if you're growing something in culture?

SCOTT DONEY: Well, yeah, these curves are mostly grown from culture.

AUDIENCE: OK. So you can really isolate--

SCOTT DONEY: Yes. Yeah, you would do these experiments in culture. But there are many phytoplankton that look more like that, where they saturate quite quickly at quite low values of CO2 gas. And the E. hux curve looks a lot more like the enzyme if you just isolate the enzyme and look at the enzyme activity.

So if you're growing-- so this is some plankton and rubisco. So in order for these other phytoplankton to have this steep saturation curve, they have to have some mechanism for concentrating CO2 at the enzyme site.

And you'll see this very creative, innovative term called a CCM for a Carbon Concentrating Mechanism. And there are a variety of ways you could do this.

For example, having carbonic anhydrase, which is the enzyme that catalyzes the conversion between CO2 gas and H2CO3, the carbonic acid, if you had carbonic anhydrase, as you started to reduce CO2 at the enzyme site, it would catalyze this equation. And you could actually draw more carbon out of the inorganic carbon system.

Another way would be-- so this would be our carbonic anhydrase. You can also have active transport, actually, the cell is expending energy in order to increase the CO2 concentration at the enzyme site.

So there's not actually a tremendous amount known about this right now. It's of some interest because if you were to look into the future, we're going to be somewhere out around-- we're currently about here. By the end of the century, we're going to be somewhere out here on this curve. If there is a big sensitivity to photosynthesis, that's a big deal. But if they're already saturated, they're already saturated. Who cares? So there is a lot of interest in this, and people are starting to try to look at in different systems to figure out what exactly is going on.

The last thing on nutrients is, you will often hear of something called Liebig's law or Liebig's law of the minimum. And Liebig was actually an agricultural-- I guess agricultural chemist. I don't know exactly how to-- he was dealing with agricultural plants, with crops.

And he was interested in the issue of-- let's say you have multiple limiting nutrients. What happens? Well, there's a couple of possibilities. One is, you can say there's some function f, that as you have this, say, a saturation curve for some nutrient x, it can take on a value of somewhere between 0 to 1.

At 0, it would be completely limiting. At 1, it wouldn't be limiting at all. So your primary production would be-- say, it would be f of x times p max. That would be for a single nutrient.

Now, if you have multiple nutrients, it could be that p would be f of x, f of y, f of z, dot, dot, dot, p max. So if x was limiting you by 50% and y was limiting you by 50% and z was limiting you by 50%, by the time you're done with that string, it would be 0.5 times 0.5 times 0.5. You'd have very low production.

What Liebig argued was that it actually should be that there's a single limiting nutrient at any time. So you'd look at the limitation due to x, limitation due to the y, limitation due to z. You'd take the one that was the most limiting, and that would set the rate.

So if you don't have enough phosphorus-- phosphorus is only there to get you like 20% growth rate, of your maximum growth rate. Doesn't matter that nitrogen might be at 30% or silica might be at 40%. It would be set by that single that single maximum. This has become-- it's now called the law.

Well, it's an empirical observation. And it's a guess that organisms would adapt themselves so that everything else-- that they would concentrate and be limited only by the thing that was most limiting, and that if everything else was a little greater than that, they could survive and limp along.

It doesn't always hold. Sometimes you'll have what's called co-limitation, particularly if-- for example, a classic co-limitation is, you need this reaction. Remember that we talked about the nitrogen reduction to ammonia.

The reductase, the enzyme that does this reduction, the enzyme system, is iron rich. And so you might have a co-limitation where there's an iron limitation on this reductase. And so your rate might depend on both how much nitrate you have there-- because that's what you're using-- but also the iron because the iron's limiting how quickly you can use that nitrate. So there are nutrient-nutrient co-limitations. You'll also see nutrient-light co-limitations.

The Liebig's law of the minimum is a good first approximation, probably better than the multiplicative approach. This would be the multiplicative. But it's not like the law of gravity.

AUDIENCE: There's [? probably ?] problems with that too but--

SCOTT DONEY: Yeah, the fifth force.

AUDIENCE: It used to work.

SCOTT DONEY: The law of gravity?

AUDIENCE: Yeah.

SCOTT DONEY: Yeah. One never knows. Maybe Congress will repeal it.

AUDIENCE: They might try.

SCOTT DONEY: I don't know. There's an apocryphal story. I don't know if it's actually true. But I read somewhere that the state of Ohio once tried to mandate that the value of pi had to be 3 because they thought it was too inconvenient for the students that it was an irrational number. But--

AUDIENCE: [INAUDIBLE] Ohio.

SCOTT DONEY: That might just be one of those-- it sounds too good to be true. So--

AUDIENCE: It does sound good.

SCOTT DONEY: OK. The last limitation is temperature. And temperature is an awkward one because-- people talk about temperature limitation. And it depends on what sort of background you come from. If you're a card-carrying biologist, we're going to define a parameter called mu, where mu is the specific growth rate.

And let's say you're some phytoplankton. Or you're a biologist measuring phytoplankton. You don't actually have to be phytoplankton to do this. Mu is going to be-- you're going to look at the growth rate of whatever organism you're looking at. And then you're going to divide it by the instantaneous biomass that you're keeping track of.

So if you're keeping track of moles of carbon in the organism, it would be the rate of change of moles of carbon divided by the moles of carbon in the organism. And so if you look at this, the units for mu-- so this is equal mu-- have to have units of 1 over time. So they're often expressed for phytoplankton in days, so like 1 over days, because that's about the generation time for phytoplankton and bacteria, is something like half a day to a few days.

So that's the common-- and it's much better than if you just did-- if you just reported things as dp dt, it would really depend on how rich your culture was, how much phytoplankton you had there. Unfortunately, this is a culture-based view. And the reason why is, in the field, we often don't know how much actual biomass there is.

So we'll talk about these photosynthesis rates. And you might try to normalize it to something. But it's often hard to figure out exactly how many viable living phytoplankton are there in the field. And so for culture stuff, you'll often see it in the form of mu. For a lot of field work, you'll just see it as dp dt, or it'll express as just a photosynthesis rate.

For the temperature. Often what you see for a lot of organisms, whether aquatic or terrestrial, is that if you plot mu as a function of temperature, you'll see some tail where they'll grow pretty low-- well, they'll grow, but not well, at low temperatures. There'll be some optimal temperature band. And then it's a very steep fall off if you go above the optimum. So it's asymmetric with respect to the optimal temperature.

That's great if you're doing individual organisms. But often, people are interested in what happens to a community. And the community will actually shift as you move through the seasons, in part because as the temperature warms up, bugs that weren't doing well-- as the temperature shifts-- and let's say it gets warmer. Some of the bugs, you've now exceeded their optimal temperature, and they die off. Other bugs, you're just kind of entering their suboptimal lower temperature range. And so they'll start to grow.

And so what you'll often see is a curve that looks more like this, which is, for a community, there's a whole collection of temperatures over which it will grow, where if you were to plot the upper envelope of that, that upper envelope tends to increase as you get to higher temperatures.

So for any particular organism, that might not be true. But for the community, as you go to warmer and warmer temperatures, growth rates tend to go up. Enzyme reactions go faster is the basic argument, that your metabolism can run faster at higher temperatures. Note the presence of warmth of warm-blooded, endothermic animals, in part because their metabolism can run faster.

In '72, Epley published an equation that he probably never figured people would use this much, but they do. If you publish a useful approximation, people seem to just flock to it-- where he said that the upper envelope could be approximated for phytoplankton as mu of t t, in degrees, c.

AUDIENCE: That's empirical, right?

SCOTT DONEY: This is purely empirical. And that gives you a pretty useful sense for, if you're in cold climates, photosynthesis is going to be low. If you're in warmer climates, it gives a doubling of about every 10 degrees. c is approximately a doubling, yeah, doubling, doubling of growth rate.

So what does this all look like if we pull this all together? We talked about--

AUDIENCE: Question-- question from MIT. What's below 0.6? Sorry.

SCOTT DONEY: Days.

AUDIENCE: Days. Thank you.

AUDIENCE: Sorry, Virginia. We can't see you.

AUDIENCE: Don't worry.

SCOTT DONEY: So at 0 degrees C, this goes to 0. The 1.066-- anything raised to the 0 power is 1. So it's 0.6 days at 0 degrees C. So it would be at 0 degrees C goes to 0.61 over day. That's for-- it would be mu. Don't use Kelvin, does awful things.

So what does this look like? We talked a little bit about-- oh. Well, there's, what does this look like, in terms of seasonal cycles? And I think I showed this the other day. There's two end members if you were to look at the annual cycle.

Often, for the Northern Hemisphere, the mixed layer depth will do something like that. So it gets deeper in the winter, shallower in the summer, deeper in the winter. And you see, in some regions, like the North Atlantic, you'll see a big bloom of phytoplankton in both the spring and the fall.

So this would be your phytoplankton. The proxy for that might be chlorophyll. And the nutrients might look like that, where this is the nutrients. And so the idea is, during the winter, you have a lot of mixing, brings a lot of nutrients up. When the mixed layer shoals, you get a bloom because of the release of light limitation. You have lots of nutrients present. That draws the nutrients down.

You have a period over the summer where you don't have a lot of nutrients. You have a lot of light but not a lot of nutrients. You have some background phytoplankton concentration. And then in the winter, when you mix down again, you kick up a little bit of nutrients. And that tends to drive a fall bloom. So this would be spring and fall.

A lot of this is based off of measurements that were made by the Scandinavians in the early part of the last century. That was where a lot biological oceanography really got its start. So that was considered canonical or normal. There are other places that have a fairly different seasonality.

And-- oh, in this plot, the primary production follows phytoplankton. So I won't draw it on there because I'll just confuse an already complicated drawing. But for example-- so this would be the North Atlantic.

But if you go to parts of the North Pacific, you see a very different pattern. There, the nutrients never get drawn all the way down. So there is a seasonality to the nutrients, but they're never reduced all the way down to 0. You see chlorophyll that looks pretty flat through the year.

But primary production shows a seasonality. So this would be primary production. And in here, something needs to be controlling the chlorophyll or the phytoplankton biomass such that even as the primary production increases sharply, the biomass doesn't build up.

So this is a region where you're focused on growth. You have these big events where you supply enough nutrients and enough light, and off they grow. And you're mostly focused on the growth term. And it's only after the bloom that you worry about the loss terms. So this is-- you might call it unbalanced, where there's a decoupling between growth and loss.

The North Pacific, the sort of opposite extreme-- and these are, of course, obviously caricatures of the real system-- is more like a steady state, where you have growth being balanced by loss. So the biomass isn't changing significantly, but the growth term is. And so there has to be a corresponding control on loss.

AUDIENCE: One more time-- like, what's causing the peak in the phytoplankton there?

SCOTT DONEY: OK. So let's say your biomass is constant all year. And your nutrients, they go down, but they're always saturating. You're always up on that saturating curve. What are a couple of things that could give you seasonality in primary production? We just went through things that control primary production. What could generate seasonality, where you get a peak in primary production in the summer?

AUDIENCE: Light and duration.

AUDIENCE: Light.

SCOTT DONEY: Light and temperature. So if you had constant biomass and you didn't have seasonality and nutrient limitation, this is what you would expect. You'd expect primary production to go up in the summer because you have more light. And you'd expect primary production to be higher, photosynthesis rates to be higher because you have warmer temperatures. Does that make--

AUDIENCE: pp is primary production and not phytoplankton?

SCOTT DONEY: Yeah, sorry, primary production.

AUDIENCE: And so why does chlorophyll stay constant then?

SCOTT DONEY: Chlorophyll stays constant because somebody has to be eating all the growth I call this-- and this tells you how much I like yard work. This is the suburban lawn hypothesis. That's not actually called the suburban lawn hypothesis any place outside of this class. But to me, this is a classic example of the suburban lawn, which is, during the summer, I have to mow the lawn, like, twice a week because the lawn is growing like crazy.

But I maintain no change in biomass by going out there every couple of days and mowing it back down flat. So this is a system where you have balanced growth, which is the more canonical term but just isn't as evocative. So you have balanced growth, where the loss terms have to be balancing the growth terms fairly closely and maintaining no net change in the biomass.

AUDIENCE: The primary production is just like total carbon fixed here?

SCOTT DONEY: Yep. Primary production would be total-- well, yeah. Usually, it's that net primary production. We're going to talk about techniques in a minute. But it's the total amount of net carbon going into the autotrophs going into the photosynthesizers, the phytoplankton.

AUDIENCE: So would you see a change in biomass and primary consumers then?

SCOTT DONEY: The assumption-- and I call it an assumption because there's not nearly as much data on the zooplankton, typically, as there are on phytoplankton. The reason is, there's a very easy assay for phytoplankton, which is chlorophyll. It's not the best assay. But it's the drunk looking under the lamppost for his keys. We measure phytoplankton and chlorophyll because it's straightforward and easy.

If you were to look at zooplankton, you would assume that your zooplankton biomass would probably more closely track primary production in the system because there's got to be a much bigger pool of zooplankton in order to keep up with the primary production. Does that make sense to you guys up there? Yes, no?

AUDIENCE: Yes.

SCOTT DONEY: OK. And we'll get back to, later in the course, why these two systems are different. But the main thought is that one of the things that's different about these is that you have probably more iron limitation in this balanced growth. And the iron limitation basically knocks all of the phytoplankton down a little bit so you can't grow as fast, so the zooplankton have an easier time of grazing you and keeping you in check.

And the bigger phytoplankton that tend to bloom, the bloom-forming species that are harder for the zooplankton to keep track of, are really limited in this system and really can't grow nearly as fast. And so that iron limitation, the proximate cause for this control is grazing. But the distal, underlying cause is iron limitation on the phytoplankton that changes both the primary production rates and the community structure, so who's there, the taxonomy of who's growing.

OK. We also might want to look at vertical structure.

Remember, if we look in depth, we tend to have light dropping off as an exponential. So this would be light. Nutrients often look like this. So you have more nutrients at depth than you do at the surface.

And you'll commonly see, particularly in the subtropical gyres, you'll see a-- it's hard to do without color, but color doesn't show up very well on the monitors. You'll see what's called a deep chlorophyll maximum.

And the deep chlorophyll maximum can have two causes. It can be caused by actual cell abundance. So it could actually be a real maximum and biomass or cell abundance. And the argument there is, well, up at the surface, I don't have enough nutrients to grow, or the phytoplankton don't have enough nutrients to grow. There's plenty of light but just no nutrients.

Deep in the water column, I have nutrients but no light. And the deep chlorophyll maximum, which is often somewhere about the euphotic depth-- so, commonly, around the 1% light level-- is kind of a happy medium, where I might have some nutrients there and some light. And I need both to grow. And so the deep chlorophyll maximum can be a cell abundance maximum because of, basically, living on the interface where you get both light and nutrients.

It can also be an apparent maximum because cellular chlorophyll to carbon ratios vary through a process called photoacclimation. Photoacclimation is if you take an individual cell, and if they are light starved, if they don't have enough light, they will increase their chlorophyll faster than carbon or other components of their cell mechanism.

Because if you're light limited, what you need is light. And so you devote-- think about it from an energy point of view. You're going to devote energy to manufacturing the chlorophyll in order to boost that up. It can also occur through photoadaptation. And these terms are get bandied about a little bit too loosely.

Photoadaptation, I think of as, there are some species that are better adapted for low light environments. And they tend to grow in the deep chlorophyll maximum. And they have inherent to them higher chlorophyll-to-carbon ratios because they're adapted to low light.

So photoacclimation is a physiological response to an individual cell or cell culture. Photoadaptation probably technically is best thought of as a cell succession, as a species succession, over longer time periods, where one species can replace another because it's better acclimated to that niche.

AUDIENCE: Can any phytoplankton acclimate to--

SCOTT DONEY: Most phytoplankton can show some acclimation. But there's a real question about how plastic cells are. So in addition to selling this book, which unfortunately I don't get any money from, I did bring down-- and just focus on the middle graph or the middle line. Let's do one at a time then.

How's that? Is that good?

AUDIENCE: Good. Yeah.

SCOTT DONEY: OK. This is panel is showing the summertime primary production estimated from space. And the way this is done is, you look at visible radiation. You look at the different colors of the radiation. Remember, chlorophyll absorbs in what? Chlorophyll is green. So what does it absorb?

AUDIENCE: Blue and red.

SCOTT DONEY: It absorbs blue and red, leaving green. If you look at the light that's backscattered out of the water, some fraction of the sunlight comes down, enters the ocean. Some of it gets absorbed by chlorophyll and by phytoplankton. But some of the remaining light actually gets backscattered out, leaves the ocean surface, and you can measure it from a satellite.

And if you look at the strength of the light and the different wavelength bands in the visible, you can actually say, well, that water looks more green than it looks blue. Therefore, it has more chlorophyll in it. It's a little more complicated than that but not that much. And it's very empirical because. We don't have excellent models for this.

Using that, you can come up with the amount of chlorophyll that's there. You can then make assumptions about light limitation and nutrients and temperature. And you can come up with an estimate of primary production. So this is a seasonal primary production. It's on a log scale, which I cut off for this purposes. But maybe we can scan this figure in and get it into the notes.

So there's almost a factor of 100 range between the purples, which are very low productivity, and the reds which are very high productivity. And so what you see is that to first order, primary production maps to regions of upwelling. In regions where you're bringing nutrients up to the surface, you have a lot of phytoplankton, and you have a lot of photosynthesis.

So you see maxima along the equator in both the Pacific and the Atlantic, maxima in the Arabian Sea because of monsoonal upwelling. This is the summer season. Along the Benguela and North African coasts due to coastal upwelling, along Peru because of coastal upwelling, and then in the high-latitude North Atlantic and North Pacific, associated with nutrients that have been brought up by subpolar upwelling and also deep convective mixing in the winter.

So you have deep convective mixing during the winter brings nutrients up to the surface. In the summer, the water stratifies, and you get a big bloom. If I slide this over without knocking my water off the table-- this is the winter season. And what you see is, similarly, at high latitudes in the winter in the Northern Hemisphere, almost no production because it's very light limited.

You still see the equatorial bands, the coastal bands. And now you see this band of higher productivity in the Southern Ocean, which is another region of fairly deep mixing where you bring nutrients up from below. What's intriguing in the Southern Ocean is that you do see possible hints, depending on which set of data you look at, that the productivity is higher downwind or downstream of land masses and some subsurface geological features.

And some people are arguing that those patterns are actually controlled by iron. This is a region where there's documented iron limitation. Iron has a fairly high scavenging rate. So there's not a lot of iron in the surface layer. And so where you have atmospheric deposition of dust, so, for example, off of Patagonia or downstream of the plateau that New Zealand sits on because of iron coming off the sediments, you might have elevated productivity.

But those are basically the general patterns or story of primary production, which is a seasonality associated with mixing and temperature and light and then also broad geographic distribution controlled by convective mixing and upwelling of nutrients.

AUDIENCE: I think I have a second [INAUDIBLE].

SCOTT DONEY: Yeah. The best satellite out there is SeaWiFS. Oops. Whoo. And if you just google SeaWiFS, you'll get more images than you want to. Yeah. As long as the instructor doesn't develop Tourette's, we're OK.

OK. So I've been talking about photosynthesis and not really telling you how we measure it.

AUDIENCE: [INAUDIBLE] really confused too [INAUDIBLE].

SCOTT DONEY: Oh, I'm sorry. There was somebody walking by the window of the classroom, making random, irrational-- I think he was calling-- yeah. Kristen thinks he was calling his dog. But--

[LAUGHTER]

Sorry. It's not that I forget you guys are up there, but sometimes the jokes just don't translate through the video link. So we've been talking about photosynthesis, but we haven't really talked photosynthesis in primary production. But we haven't talked about how we measure it. And this is not a methods class. But what we're going to find in the next couple of lectures is that we're going to start defining particular processes. And they're somewhat operationally defined.

And so you really need to have some understanding of how they're measured so that you can understand how they're interconnected. Because there are classic things that sound like they should be giving you the same results that they're measuring, the same broad parts of the elephant. The picturesque is a group of blind people walking around an elephant, trying to figure out what it is.

You think you're all measuring the tail, but you're measuring it in different ways. And then you get inconsistent results. And the reason is because the way you're measuring them is measuring is truly actually measuring different aspects of the system. And so we're going to go through some description of primary production to give you some broad ideas on that.

There's a few main ways. One would be, if you remember, photosynthesis-- oops, writing it the wrong way-- CO2 plus water goes to carbohydrate plus oxygen. That was the basic equation. So there's a couple ways we could attack this.

We could measure the formation of the carbohydrate. We could measure the loss of CO2. Or we could measure the production of oxygen. We're not going to deal with water because it's an aquatic system, and it would be way too hard to track the water loss.

Or we could look at light absorption utilization. Because there actually is a light term in the forward in the forward reaction. The initial work was done by [? Gran ?] starting around the end of the First World War. And they were doing incubations of the change in oxygen over time in light and dark bottles.

So these would be incubations that were done in a laboratory. You would inoculate a certain amount of phytoplankton. You would then close up the bottle. Well, you'd inoculate the phytoplankton, measure the amount of oxygen that's there at the beginning time, close the bottle up, either put them in the dark or put them in the light, and then measure how much is there a day later, for example.

And the limitations on this, of course, are that you need to have a big enough signal so that you can actually measure a drawdown of oxygen. So this was pretty good for coastal systems, not so good for open ocean systems because you just didn't have a strong enough signal because there just wasn't enough phytoplankton there.

Also, this was around the time of the introduction of or the use of the Winkler O2 titration. So there were fairly good, precise ways of measuring changes in oxygen with the Winkler titration.

And let's see. Nielsen in 1952 introduced the C14 carbon fixation approach. So this is-- you take an add radiolabeled CO2 to your system.

That gets formed into radiolabeled organic matter. And you measure how much radiolabel ends up on particulate organic carbon. So the idea here is, you spike something with radiolabeled C14 inorganic. After some period of time, you grow them again in dark and light.

So you can look at the dark as your control to see if there are any effects due to absorption or problems like that. And then you would then filter the sample and then put it in a scintillation counter and count how much radioactivity is on your particles. And you'd have to be very careful to make sure you got rid of all the seawater that's on your filter. So you might actually acidify your filter to drive off any radiolabel that ends up in your inorganic carbon pool.

Other than the fact that-- well, there's two issues with this. One is, if you do this, you're going to be in a constant battle with people who want to measure radiocarbon in the natural environment. In fact, at WHOI, because we have a big accelerator that measures radiocarbon at natural abundance levels, there's sort of an informal ban for people from walking from one set of buildings to another set of buildings because of cross-contamination issues.

It is actually a serious issue. But that's more that's more social than it is analytical.

AUDIENCE: Like change their shoes?

SCOTT DONEY: Yeah, changing your shoes or going home and not coming back until you've showered and changed your clothes. One problem is that this technique typically only measures particulate organic carbon. I want to go on to a next page for this.

So you've got this 14 CO2. It gets taken up into 14C organic matter. Now, if you ran this reaction instantaneously-- so if you were able to spike the sample and measure it a millisecond later-- and, presumably, everything was well mixed-- the only reaction you'd be measuring would be this forward reaction.

Because there would be so little production of organic matter that has this radiolabel. You use high enough values that you don't worry about the natural background, that you won't have any loss of this. And so that would be an instantaneous measure of. gross primary production.

Remember, gross primary production was photosynthesis. Net primary production is photosynthesis minus autotroph respiration.

The problem comes because of the finite duration of the incubation. You have to run it long enough so that you get a big enough signal to actually see. But if you start to run it for, let's say, 24 hours or 12 hours-- those are the two common ones, are 12 hour-- you'll hear it as dawn to dusk-- or 24 hours.

Some of this radiolabeled organic carbon might have other fates than staying in particulate. It might start forming radiolabeled DOC. And typically you only are looking at the stuff that's filtered onto particles, not in the dissolve pool.

So if you're doing this technique, the C14 primary production technique, if there's a substantial production of DOC, you'd actually be underestimating your total photosynthesis rate because you'd be missing the fraction that ended up in the dissolved organic pool.

If you ran it for long enough, you'd actually start having the back reaction, where some of this organic matter would then be respired. And that can be a problem if you have a lot of photorespiration, where you're forming organic matter and then you're respiring it right away.

It might not be that the whole cell has to become radiolabeled but that certain metabolic pathways get radiolabeled and so that you lose organic matter fairly quickly. Those are both complications. And the C14 technique generally, although it's the most widely used, is somewhere between GPP and NPP. It's not truly NPP. It's not truly GPP. But it's what's most commonly measured and what's compared against.

When they first started doing this about contamination-- and this is especially true for open ocean plankton. Open ocean plankton are used to relatively low trace metals. And in a lot of the bottle incubations, you were getting contamination that led to underestimates in primary production because of trace metal poisoning.

And so there's been a lot of effort, back in the 1970s, to develop trace metal clean techniques for your C14 work. And they think they've gotten around most of the bottle incubation effects. But a lot of the older data is suspect.

Where did I get last year? OK. There are a couple of other techniques that are used.

There is an O18 technique. And the idea there is-- remember, one of the ways would be to look at oxygen production. But oxygen production has some of the same issues. If you run an incubation and you're producing oxygen, anybody who's respiring, who has respiration, not just the phytoplankton, but also any heterotrophs, are going to be reducing oxygen.

So you could have a lot of photosynthesis but very little growth in oxygen in your container because somebody else is respiring at the same time. But if you spike the water and do this in heavy water and then measure the O18-O16 ratio in the oxygen, you can really get at just the forward reaction.

And the reason why it's the forward reaction is, so little of your water is being used up that there's really little effect. Very little of the water's used up. Very little of the oxygen is changed because you have a lot of oxygen, typically, in the container. And so you can't really affect or back affect the reaction of your 18 oxygen if you use a big enough spike.

And so this O18 spiking incubation really is probably one of our best measures of gross primary production. It's not commonly done. It's done a handful of times. Probably for every 100 cruises with C14, somebody does O18. But it does give some idea where then you can go and look at the correction for GPP to C14 NPP.

So you could make a correction for what the true gross primary production is relative to the C14 measurements that are being made.

AUDIENCE: That's just because it's a lot harder to do that technique than the--

SCOTT DONEY: Yeah. The C14, you can do by scintillation counter. This, first off, you're dealing with gases. So before, you're just filtering water and putting particles onto filters. Here, you actually need to do it in a gas-tight system, where you can keep track of that you're not having gas exchange during the experiment. Then you need to run this on a gas-proportional mass spectrometer. They're not nearly as common as scintillation counters. It's just it's a lot more work. Also, and this is expensive.

AUDIENCE: Just to make sure here, the reason this works is because the oxygen from the water goes into oxygen gas rather than the organic matter.

SCOTT DONEY: Right.

AUDIENCE: I Just wanted to-- it's something we were questioning during generals.

SCOTT DONEY: Yes. In photosynthesis, one of the oxygens in O2 is coming from water. Remember, CO2 plus water goes to CH2O plus O2. So it's that.

There have been a lot of advances in making DIC measurements and also oxygen measurements. So people are starting to do a lot more computer-controlled titrations of the changes in DIC and oxygen.

So unlike [? Gran's ?] original experiments, where there just wasn't enough signal for him to measure, people can start to look at diurnal changes in DIC and oxygen, both in incubations and in the field.

And gas exchange really isn't fast enough to equilibrate the water on diurnal timescales. So the diurnal drawdown if you looked at the diurnal cycle in the water-- let's say DIC was high in the morning, low and then high and then low. That would give you a pretty good estimate for photosynthesis because you could back out and say what respiration was at night.

And so people have been trying to do that from the field to get away from doing bottle incubations, where anytime you collect an organism from the water column, there's a chance that you're going to screw it up and you're going to perturb the system.

And then finally, we're not going to go into a lot of the details for the bio-optics. But the basic idea for the bio-optics is as follows.

You have photons coming in. So this would be a photon. There's lots of different pathways that photon can take. It can heat the water. It can be absorbed by detrital junk, that [INAUDIBLE] stuff. But some of them are actually going to hit a phytoplankton and be absorbed.

And if you knew how much was absorbed and then what the fate of that absorbed light is-- so that can go several pathways. So the absorbed photon, it could go to heat. You could just start cooking your phytoplankton. Some of it could be fluoresced-- that's not spelled right.

That's supposed to be fluorescence, basically readmitted at a different wavelength. Remember, chlorophyll absorbs in the blue, emits in the red. Or it could be going to chemical energy for photosynthesis.

So if you were able to understand and compute how many of the photons are actually being absorbed by phytoplankton and then able to partition how much of those absorbed photons are going into these different pathways, you would be able to then say something about how much photosynthesis rates are, which is this right here.

Now, one of the really clever techniques that's been invented is it's sometimes called pump and probe or variable fluorescence, variable fluorescence.

Basically, it's the idea that-- let's say you have your chlorophyll antennas. At any one particular time, many of these antenna are open at the reaction sites.

And so a photon comes in. And some of it's going to get dissipated by heat because it's just a dissipative system. Some of it's going to go to chemical energy. But if you added enough light to the phytoplankton, you would actually fill up all the reaction centers.

So let's say you're measuring your phytoplankton. And then you start giving it enough light so that you very quickly, on short time scales, you fill up all the reaction centers so that none of the reaction centers are open. They all have just received a photon. They can't receive another photon. They can't accept another photon for a certain amount of time because it takes a certain amount of time for the reaction centers to process that photon and reset themselves.

If you looked at the change in fluorescence before and after you've closed all the reaction antenna, that would give you an idea of how many antenna were actually open and ready to accept a photon. Because before you've done this-- let's say some of them are going to heat, and some of them are going to fluorescence, and some of them are going to photosynthesis.

But after you fill the reaction centers, the argument is, well, the same amount is going to be going to heat. You're then going to have this huge amount going to fluorescence because there's no other pathway for them to go. And you'd have zero going to photosynthesis.

And by that pathway, you can then back out what the photosynthesis rate would have been before because you now know how many reaction centers were absorbing light. So it's pretty clever. It's just being developed over the last 10 or 15 years. And it nicely complements the C14 work. Because instead of focusing on the organic products, you're now looking at the light.

I just wanted to show this, if I can fit it on here, this last figure. Oops. And then we'll wrap it up for the day. This is a summary plot out of this book I was showing earlier for primary production from the seven US JGOFS process studies and time series sites.

And so it's primary production-- or photosynthesis, if you like-- in millimoles carbon per meter squared per day. This is measured by C14 in all cases. These are different environments. And the values range from-- down about the triangles are the means. The circles are the maximums. And then there are standard statistical ranges.

Typical primary production values are somewhere between, say, 20 and 30 millimoles carbon per meter squared per day, with peak values during, say, bloom seasons as high as 100 to 150. And so that gives you a scaling for what to expect. Great. So what we'll do is, we'll start talking about export production and new production and net community production on Thursday.