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**SCOTT DONEY:** We're going to transition-- we're going to have, now, a set of six lectures on the water column. So we've been-- if you like, we've been looking at all of the ways that material gets into and out of the ocean, so hydrothermal vents, rivers, air-sea-gas exchange, particles. Is there a thermostat in here we could--

**AUDIENCE:** He turned the heat off when he got here.

**SCOTT DONEY:** Oh, he did? OK. What we're going to be focusing on next is actually the dynamics in the water column itself. And so we're going to start by having a set of lectures on photosynthesis. That will be the main focus for today, and a little bit into next Tuesday. And so the photosynthesis is in the upper, illuminated part of the water column.

We'll then have some lectures where we look at what happens to that material once it's formed from photosynthesis. So we'll look at respiration terms, and then what's left over, which is the export.

So organic matter is formed by photosynthesis. The bulk of it is actually respired in the surface layer. The part that isn't respired is either advected away or sinks as particles. We usually call the stuff left over as export because you can think of it as local production, and the material that is in excess gets exported out of those local conditions. That exported material is then going to respire at depth, and then some small part will end up in the sediments.

We'll be starting out looking at-- the focus will be on carbon. But we will also fold in nitrogen, phosphorus, oxygen, some of the key limiting nutrients, and also oxygen since it's often used to understand photosynthesis and respiration. We'll have some talks that we'll look at the internal dynamics of calcium carbonate in the water column, and then also the silicate cycle, which is associated with biological formation of particles and sinking. So over the next-- over the next six lectures, we will cover all of these topics.

The class notes are-- you'll get both PDFs of my lecture notes that I use to give the lecture, but there are also some older, typed lecture notes that have been posted on the web. We don't have the electronic figures that go with those because those are older notes from back in the prehistoric days when this course was taught on overheads and lots of xeroxes.

The notes are really useful, but just be aware that they don't have figures. I'm trying to dig up and see if maybe we can get those figures scanned in to go with those lecture notes, but bear with us on that. So in terms of things for the exam and stuff, all you will need to know is what's being taught in the course, but you can use these older notes as background-- as background material.

So today, we're going to cover-- start in on primary production, or photosynthesis. And if you're a biologist, bear with me because we're going to skim through a lot of biology in a fairly short period of time. Everything I say is hopefully correct, but it's not as detailed as you might learn in a full biological full course on marine ecology or biological oceanography.

The basic reaction we're looking at here is the conversion of CO<sub>2</sub> plus water in the presence of light. So H<sub>2</sub>O, to some form of organic matter plus oxygen. This is typically called-- or can be called photolithotrophy or photolithoautotrophy. It's, photo, because the main energy is coming from light, so this is the energy source. It's, litho, because you're using-- the primary carbon source is inorganic. And it's autotrophic because you're creating that organic matter.

If, instead, we had used, for example, chemotrophy-- would be a case where you were using-- instead of using light for the main energy source, you might be using some form of organic matter. So you could have chemolithotrophy, where your carbon was coming from inorganic forms, or you could have chemoorganotrophy, where you were actually taking your carbon source from organic matter as well as your energy source.

So there's a whole series of these. In most of the upper ocean, we're going to be looking at photolithoautotrophy, often just called photoautotrophy, or even abbreviated as autotrophy. The reverse of this reaction, if we were to write that reaction backwards, the C organic plus O<sub>2</sub> into CO<sub>2</sub> plus water, is respiration.

The main way that photoautotrophy is carried out in the surface ocean-- almost all of the organisms use chlorophyll as their main pigment for absorbing the light. So remember, the equation is you're taking light energy, and you're using that light energy to form organic matter out of inorganic carbon.

The chlorophyll molecule-- put this over here so I can see it-- is a tetrapyrrole. Let's see if I can do this without-- so it's a magnesium ion surrounded by nitrogens, and then those nitrogens are in a-- in pyrroles.

I guess the main thing you need to know about this is that the reason why-- and this is a long-- this is a long carbon chain down here. What makes this useful as an antenna for absorbing light is that the electrons in this organic framework surrounding the magnesium are distributed. These double bonds-- I could write this with a slightly different configuration where the double bonds were switched, moved over one.

And it's actually a series of pi orbitals, where the electrons are actually distributed over the entire molecule. So the electrons are not isolated to a single bond. They're actually shared across the entire pyrrole. Because of that, it allows for-- it allows for easy electron transitions so you can get a photon that comes in and then bumps one of these electrons in the pi orbitals up to a higher electronic state. And so that's how you're absorbing-- you're absorbing a photon in the visible into the chlorophyll pigment.

So light comes in. And you're converting light energy into an excited electron, and then that excited electron is transferred out of the chlorophyll through a series of enzymatic reactions, where it can then be-- that energy of the excited electron can be used to break and form chemical bonds.

In addition to chlorophyll-- this is actually chlorophyll A. There's a whole series of what are called accessory pigments. Oh, I should just say you'll also sometimes hear this as, conjugated double bonds, double bonds. There's a whole series of accessory pigments. So for example, chlorophyll B, chlorophyll C, carotenoids, biliproteins.

These accessory pigments do a variety of different things in the cells. The main antenna is typically chlorophyll, but sometimes there are accessory pigments that also absorb light at different wavelengths, and that light can then channel down and be used by the chlorophyll process because it's basically transferring the excited electron down into the reaction center of the antenna.

They also have use for protection, for photoprotection. A lot of times, these pigments are there in the cell to protect the cell from either UV radiation or from other radiation from damaging the chlorophyll reaction center. So the main thing about accessory pigments is they absorb light at different wavelengths than chlorophyll.

So if I were to draw a absorption spectrum for chlorophyll A, as a function of nanometers-- so this would run-- that's in nanometers. This would run, in the visible, from 400 to 700. You're going to see a peak in the blue and then another peak out in the red.

So what's going to happen if you have a pigment that's absorbing in blue and red? What light is left over? What light are you actually going to see? Green, right? So this is blue. This is red. And then you have-- then you have green. And the accessory pigments can fill in in this middle region. And so they can actually channel photons that aren't absorbed by chlorophyll and provide energy into the cell in some cases.

This band of, say, 400 to 700-- sometimes you'll see it written as 350 to 700-- is called PAR, which is the-- PAR is the photosynthetic available radiation. And it's typically 45% of total solar, somewhere around in that range. It does depend upon clouds and time of day and solar zenith angle, but that's a pretty decent approximation. So about half the solar light that's coming in can be used by the photoautotrophs. The other half basically goes to warming the-- warming the water.

**AUDIENCE:** Wait. So about half can be used, or about half does get used?

**SCOTT DONEY:** A half can be used. Yeah. Only a small fraction actually gets used in photosynthesis, but only about half is available. The other half is just-- it's gone because the photons don't have enough energy to be used in photosynthesis.

You don't think of the cell as having dissolved chlorophyll. The chlorophyll is actually highly organized within the cells, within membrane structures. And in fact, the chlorophylls are an antenna, where you have something on the order of about 500 chlorophyll molecules for a single antenna. And within that antenna, most of the chlorophyll are just there to absorb light, and then they transfer these excited electrons down to what's called a reaction center.

And it's at the reaction center that that electronically-- that excited electron is then transferred into enzyme systems that can do actual work for the-- work for the organism.

There's two parts to the photosystem called Photosystem I and Photosystem II. And I don't expect you to know the full details of these because these get rather complicated. But you should know that there are these two different photosystems, and they have different functions. Photosystem I is involved in the reduction of a molecule called NADP.

And NADP stands for nicotinamide adenine dinucleotide phosphate, which is a bit of a mouthful, which is why we typically call it-- typically call it NADP. So when you reduce or NADP, it goes to NADPH, where you've actually added a proton to it.

Photosystem II is involved in the liberation of oxygen from water. And the two are actually coupled so that you can think of this as a chain, where you need both Photosystem I and Photosystem II to be functioning.

If you combine them and look at the net effect of both of them, the reaction looks something like this under light conditions. You're taking two waters plus four NADP-plus with approximately eight photons, going to oxygen plus 2-- oh, why did I write 4 over there? Sorry. I'm having a brain fart. This is a 2. Can't even read my own notes. NADPH plus two protons.

In addition to reducing two NADPs, you also generate four ATPs. So you take four ATPs plus four inorganic phosphate, and you form four ATPs. Now, ATP is the basic energy currency within the cell. ATP is adenosine triphosphate.

ADP has two phosphate units on it. ATP has three. You're storing energy in that bond between that third phosphate unit, between the second and the third phosphate unit. And so in the process of forming ATP, you're storing energy in that ATP. That ATP can be used later by enzymes to drive reactions that require energy. So this is how the cell generates energy. So far, we've liberated oxygen, and we've generated reducing power and stored chemical energy. So this is your reducing power. This is your energy.

But we haven't made any organic matter yet. To make organic matter, there's a series of what are called the dark reactions, or the Calvin-Benson cycle. And these are involved in the formation, the actual formation of organic matter. So the reaction is two protons plus CO<sub>2</sub> plus two NADPH, goes to some generic carbohydrate. We'll get to that in a moment.

So this is a generic carbohydrate plus water plus two NADP-plus. So essentially, you use your reducing power to reduce the oxidized form of carbon to a more reduced form in the form of the organic matter. And this uses up three ATPs-- ADP plus 3 P-I. Notice that there is a difference. This generates four ATP. This generates three ATP, or uses up three ATP. There is an extra ATP that can be used within the cell. And it depends on what you're synthesizing and all sorts of things like that.

The net reaction, if you combine the light reactions and dark reactions, are CO<sub>2</sub> plus two H<sub>2</sub>O goes to-- with approximately eight photons. Now, I say approximately eight photons because not all the photons absorbed end up being used biochemically.

For example, you can lose photons by fluorescence. Chlorophyll fluoresces. In fact, that's one of the ways you make measurements of chlorophyll, is you shine a beam of light into a seawater sample. You shine a beam of light at one wavelength, at a high energy of photon. Some of those photons are absorbed by the chlorophyll, and then they fluoresce. They re-emit a photon at a different, lower wavelength.

And that can be a very accurate or a very precise measurement because you're measuring photons at a different wavelength than you're putting them into the system. So it's not- you're not measuring the absorbance, where you have to worry about scattering of photons and all sorts of things like that. You're actually looking at a distinct signature that's specific to chlorophyll, which is that re-fluorescence at a different wavelength.

But some of the photons absorbed by the chlorophyll, depending upon the conditions, might just get re-fluoresced, or they might be lost into heat. So not all the photons that get absorbed by the chlorophyll antenna end up driving this reaction forward.

Another thing is I've written this generic carbohydrate, but the cell needs a whole bunch of things that are carbon-based. It needs to make sugars, which go into carbohydrates. It needs to make amino acids, which go into proteins. It needs to make fatty acids, that go into lipids. And it needs to make nucleotides, that go into DNA.

The amino acids and the nucleotides have a lot of nitrogen in them. So in addition to carbon, you also need nitrogen to form amino acids and nucleotides. And if you actually look at the cell's biochemistry, they're going to have-- this equation is going to be slightly different, depending upon what it's making.

So for example, if I were making a fatty acid-- oh, well, let's go back for a second. If I look at this reaction, I can define something called the photosynthetic quotient. And photosynthetic quotient is just the ratio of O<sub>2</sub> to CO<sub>2</sub>. So it's the ratio of the O<sub>2</sub> that you produce per CO<sub>2</sub> molecule that you consume.

And so for this reaction here, the PQ would be 1. But in fact, the PQ for most algae and photoautotrophs is greater than 1, and it's because you're forming, for example, fatty acids or other compounds. So a fatty acid might look like-- and the photosynthetic quotient for that would actually be more like around 1.42, rather than 1.

And so there's been a lot of work within the community to try to come up with an estimate of the photosynthetic quotient for phytoplankton. And there's two ways to do that. One is just to take your algae and essentially burn them, add oxygen until you've taken all the organic matter and converted it into CO<sub>2</sub>.

The other way is to look at the water column and to see what-- when you change inorganic carbon, what's the relative change in oxygen. And we'll talk about that more when we get to remineralization, about different techniques that have been used for that.

But the canonical numbers are that the oxygen-to-CO<sub>2</sub> ratio for algae is something in the range of 150 to 170 over 106, where you have a ratio that looks something like this, where you have C 106, some number of hydrogens, oxygens, nitrogens and one phosphate. So this would be a canonical algae organic molecule. There is, of course, no organic molecule that looks like that, but that's what the composite might look like.

A lot of this work dates back to Alfred Redfield, who was a professor of physiology at Harvard and was also one of the first marine chemists here at WHOI. And, in fact, the Redfield building is named after Alfred Redfield. These are sometimes called Redfield ratios. When we do nitrogen and phosphorus, we'll come back to this in more detail.

Most of the focus has been on the nitrogen to carbon, the phosphorus to carbon, but the oxygen to carbon is equally important. And it's still not actually fully resolved. It probably varies in time and space, depending upon what the community-- who's there and what kind of environmental stresses they're under.

So that's photosynthesis. The reaction, CO<sub>2</sub> plus water, under light conditions, to organic matter. The forward version of this reaction is often called gross primary production. You'll sometimes hear it called GPP. And it's just jargon. The problem is typically, we don't measure gross primary production because the cells also need the autotrophs respire some of the carbon that they make for energy.

So for example, at night-- during the day, they photosynthesize. At night there's a basal metabolism or a basal respiration. So if you were to watch a cell at night, the cell would actually be consuming oxygen and using organic matter. That's also going on during the day. It's just very hard to see with normal techniques. And we will talk, I think on Tuesday, more about how these measurements are actually made.

So what we typically measure is something more like what's called net primary production, which is GPP minus the autotroph respiration. For most systems, the autotroph respiration is pretty small. They're fairly efficient, so it's often less than or equal to 0.1. The respiration is equal to less than or equal to 0.1 GPP.

But for example, there are systems, for example, in the tropics, in oligotrophic regions, where it can get up to 0.4 GPP. And some of this is what's called photorespiration, which is simply the cells-- they have the antenna there for absorbing light. They're driving the reaction this way, but they don't have enough nutrients to form all the other parts of their cells that they need. They don't have enough nitrogen and phosphorus to build amino acids and DNA.

So they can't replicate themselves. They can't grow new cells. And so they just churn out-- they just recycle that organic matter. So sometimes, in some environments, respiration can get rather large. Any questions so far? Nope. OK.

So who are these autotrophs? There's something like about 20,000 phytoplankton species. And I'm going to put "species" in quotes because unlike mammals or reptiles, it's often hard to define what a species is. And in fact, one of the rather well-known and well-studied phytoplankton species, prochlorococcus-- when they actually went in and started to look at the genome of prochlorococcus, they found a variety of different strains, and the genomic differences between them were rather stunning. Huge amounts of differences in the DNA code.

And then that raises the question of, really, are these actually-- are these truly ecotypes or variants of the same species, or are they very different species that just happen to look approximately the same to us because we're looking at very small cells, and the techniques we're using are rather crude to characterize what is a species?

So the paradigm number is 20,000, but this is a really loose definition of what a species is, particularly because a lot of the bacterial species, in particular, are able to exchange genomic information across species boundaries quite readily. And so you'll see lateral gene transfer, which begs the question of, well, what's a species, then, if they're able to exchange genetic information?

There are, however, some significant differences that allow you to at least group these species into some larger groups. One of the big ones is prokaryotes, or prokaryotic cells, versus eukaryotic cells. The prokaryotes don't have a defined nucleus within their cell. Eukaryotes do have a defined nucleus.

And in fact, the best understanding for most of the phytoplankton is the way cells became eukaryotic was there was some form of endosymbiosis, where one prokaryotic cell basically swallowed or engulfed a second prokaryotic cell. And there's been a series of these endosymbiotic events through evolutionary time. And that's how not only did the eukaryotic cells get nucleuses, but they also got things like mitochondria and other internal organelles, chloroplasts, mitochondria.

The big difference is, in the eukaryotic cells, the nucleus is where most of the genetic material is. The mitochondria actually can have their own genetic material. But you need some biochemical mechanism for transferring the proteins that are made in the nucleus, or, excuse me, the genetic information that's made into the nucleus back out into the cell. And it's a little bit more complicated in terms of the internal biogeochemistry.

Prokaryotes tend to be smaller than eukaryotes, but that's not always true. There's one really bizarre prokaryote, and I can't remember its name, but it was found off of the sands of Namibia, and it's actually visible with the naked eye. It's like one of those weird things out of science fiction.

With what you might then call the eukaryotes, there are a whole series of different groups that all are considered phytoplankton. They're not very closely related if you look at them genomically. Oh. Within the prokaryotic, let me just say, one of the big ones are cyanobacteria. You'll hear about cyanobacteria a lot. So for example, prochlorococcus is a cyanobacteria. Trichodesmium is a cyanobacteria. They're quite prevalent as photoautotrophs, particularly in oligotrophic regimes.

In eukaryotes, you have both green and red. Green. That was green. Green and red algae are the diatoms. And dinoflagellates are part of the red algae. You also have haptophytes, which are where the coccolithophores fall. Coccolithophores are the ones that form little calcareous shells.

And I have some-- I have some pictures of some of these things. So this top image is a synechococcus cell, which is a type of cyanobacteria. It's quite small. This is a half a micron. At the other end of the spectrum is trichodesmium, which is a colonial nitrogen-fixing cyanobacteria. These are actually visible by the naked eye, not individual cells but the whole colony, and you can actually pick them out by hand.

This is the silica shell from a diatom. Diatoms form little, almost like pill boxes or hat boxes. There's two shells, silica shells, that nest in each other. This has a thickness. If you turn it on its side, it would look like a wafer. And then I should say diatoms come in all sorts of shapes. Some of them look like these little pill boxes. Other ones look more like elongated capsules. And they can be either-- live alone, or they can-- or they can live in colonies, in colonial form. They form long chains, often.

This is an electron micrograph of a coccolithophore. So you see these little ovals. Those are actually little-- they're called coccoliths. They're little calcium carbonate plates that surround the shell, or surround the cell.

And in fact, when you have a bloom of these, when the bloom starts to die off, often, they will lose these lifts. And it's like-- the water looks like-- water a off of a glacier that has really fine glacial flour. It gets this really pretty looking. greenish blue, milky color. And that's because these are scattering-- these are very good at scattering light. They're small, very fine bits of chalk ground up. Think of it as ground-up chalk in the water. And you can actually see these from space because of the amount of backscatter you get in the visible.

And then there's a whole series of other smaller groups that have all-- they're all phytoplankton, but they haven't evolved from a single group. They've evolved multiple times from multiple different directions within the eukaryotes. So it's a very phylogenetically rich group of species. And so you need to be very careful about talking about the typical phytoplankton. And I will, for the rest of the course, talk about phytoplankton as if it were a single group of organisms, but it's not. It's quite diverse.

Another way that you can look at phytoplankton is size. And size is quite important for a variety of reasons. One is grazing. Typically, but not always, grazers eat things that are smaller than them. Not always true, but for the most part. And so if you're big, one way to avoid grazing is to be bigger than the zooplankton or the heterotrophs that are there.

A second is export. If you're really, really small and you die, you won't sink very fast. And so you don't contribute that much to export flux. Or even if you're gray, somebody eats you and turns you into a fecal pellet-- well, if you're small, your grazer is going to be small, and your grazer isn't going to produce a very big fecal pellet. Well, small fecal pellets aren't going to sink very fast either. And so size has a strong correlation with export production.

There's a size classification that's based on diameter. And they go up by about a factor of 10 in diameter, but a factor of 10 in diameter is going to be a factor of what in volume?

**AUDIENCE:** Roughly 100.

**SCOTT DONEY:** Roughly 100. How about 1,000? Because it's going to be-- the simplest assumption would be it's a sphere. Of course, they're not always spherical. So even within these ranges, there's actually a huge range in cells. But picoplankton are about-- maybe 0.2. That's pretty small. Most bacteria-- you only get below a micron when you're a heterotrophic bacteria or a prochlorococcus or maybe a synechococcus, pretty small things, up to about 20 microns. Nano is 2 to 20 microns. Micro is 20 to 200. And then you have meso and macro, et cetera.

These are pretty loose. People will talk about the piconanoplankton, and they might not have gone out and actually measured the exact size, but it gives you a rough-- a rough ballpark figure.

The last way we distinguish-- that was size. The last might be by what you might call guild or-- and this is-- some of this is ecological, but some of this is geochemical. For a geochemist, I might want to know everybody who can fix nitrogen-- can fix nitrogen, right? Because that's a very important geochemical process. Nitrogen fixation is converting into gas, which is unavailable to most organisms, into a form that can be used by most organisms, nitrate, ammonia.

I might want to know about calcifiers. Who forms a calcareous shell? Totally different groups might be calcifiers, but I'm just interested in whether they're forming calcium, calcium carbonate. Similar, siliceous, shell users, et cetera. So you can also group things by these geochemical functional groups.

So that's who's there. The next question is, what controls photosynthesis? Well, the first thing is just phytoplankton biomass. If there are more of these autotrophs there-- oh, and I should note-- I'm trying to be very careful and not call these, plants, because remember, we were talking about how many of them are prokaryotes? Well, the plants are only-- you can have eukaryotic plants. The prokaryotes are not plants.

People get a little sloppy, and they call all of them, microscopic plants. Well in much of the ocean, plants are actually a minor contributor. I don't know. It's one of those little biological quibbles. But I think it actually is important to distinguish that most of the photosynthesis, for example, in the oligotrophic gyres is being done by prokaryotes, not by eukaryotes. So they're not technically plants.

So the first thing is you need to know how much phytoplankton biomass is there. And it's somewhat circular because the amount of biomass is going to depend upon photosynthesis in the past. If you've had more photosynthesis, you can build up more biomass.

But it's also going to depend upon grazing, sinking. Some of the larger phytoplankton actually have a sinking rate, or they will get to an end of the bloom, and they will sink out. And mortality, and within mortality is natural mortality, but it also might be, for example, virus, lysis. And there's actually a fairly dynamic interaction between viruses and phytoplankton.

Second thing you'd need to know is how much light there is. Obviously, more light, probably more photosynthesis. Nutrients, the amount of inorganic carbon or CO<sub>2</sub>. And we'll talk about that as well. And then finally temperature. So we're mostly, today-- we're going to start into light. I don't know if we'll get all the way to temperature. Depends on how things go. But we'll go through these individual controls. We'll talk more about phytoplankton biomass on Tuesday when we start looking more at the whole community.

So phytoplankton can only grow in the upper ocean. And if you imagine that if we were to plot versus depth, you have some surface irradiance. As an approximation, that irradiance is going to drop off, approximately, exponentially, with depth.

And at some point, in the water column, the irradiance is going to equal 1% of the surface irradiance. That was-- is typically called-- that depth, where you reach 1% of the surface radiance, is called the euphotic zone. And to first order, most of the photosynthesis, or the vast majority of photosynthesis, is going to occur within the euphotic zone. It's going to occur above this euphotic depth, the 1% light level.

This euphotic zone, in very clear waters, might be 125 meters, and in very turbid waters and very turbid coastal waters, with either a lot of phytoplankton or a lot of other sediments or detrital material, might be a few meters. So there's a large range.

I mentioned that you can approximate this as an exponential. For a single wavelength, the irradiance, as a function of depth, can be approximated as the surface irradiance times  $e$  to the minus  $k$ -- oh, sorry. Let me start that over.  $e$  at a depth,  $z$ , for a particular wavelength,  $\lambda$ , is going to equal  $e^0$  for that particular  $\lambda$ ,  $e$  to the minus  $k \lambda z$ . It's just going to be an exponential falloff.

It's going to be different for different wavelengths. So  $k$  as a function of  $\lambda$ -- typically, the things that are going to absorb light in seawater are water itself, chlorophyll, and what's called CDOM, which is chromophoric dissolved organic matter. Sometimes you'll hear of CDOM as gelbstoff, gelbstoff, which is basically yellow stuff, otherwise known as a bunch of organic crap that they didn't know exactly what it was, but it was absorbing a lot of light and making a mess out of their experiments.

In most waters, the reds get absorbed early, so red light disappears rather quickly. So if you go out to the very, very clearest open ocean, if you go diving in the Sargasso Sea, the water looks very, very blue, and that's because you've absorbed most of the red-- most of the red light. If you have a lot of chlorophyll, you'll also be absorbing in the blue because the chlorophyll absorbs in both the red and the blue. So if you have a lot of biomass, you'll also start soaking up the blue. So there are spectral shifts with depth.

And so this equation, while it might hold well for a particular wavelength, is only an approximation. You'll sometimes see it written as this, approximately,  $I_0 e^{-kz}$ , where this is now integrated over PAR. And that's only an approximation because some of the wavelengths are being absorbed differentially.

The last thing on this before we look at actual photosynthetic irradiance curves is that this  $k$ -- for example, if I were to write out  $k$ , you would have a term for  $k_{\text{water}}$ , plus a term for  $k_{\text{chlorophyll}}$ , plus a term for  $k_{\text{CDOM}}$ . And often, it's linearly separated like this in two different absorption terms. If you actually get into this specific field, you need to worry about not only absorption but also scattering. A lot of the light gets scattered.

And so you can have-- when light scattered, it comes at a different angle, and it can get absorbed. I mean you increase the path length over which absorption can occur. And so actually doing this can be a fairly complicated process if you want to do it from first principles. A lot of these are actually what are called effective absorption coefficients because they're not the real absorption if you were to put it in a cell and measure it over a very small cell length, but they're the effective absorption, including all the effects of scattering light within the water column.

So how do phytoplankton respond to light, in terms of their photosynthesis rates? What people often do is they take a phytoplankton culture or a phytoplankton sample, and they expose it to different levels of irradiance. And then they measure the photosynthesis rate, and they make what's called a PI curve, for photosynthesis irradiance curve.

You will go back and forth. Sometimes the literature uses  $I$  for irradiance. Sometimes it uses  $E$ . And there are very strong opinions about which you should use, and I'll leave it at that. And people have their good reasons for using different things. But in this class, I'll just talk about  $P$ -- use it as PI.

Typically, the curves look something like this, where you have a region right near-- in very low light, right near the intercept, where it's approximately linear. So photosynthesis scales linearly with irradiance. You have some region that highlight where it saturates. And then you have, potentially, a region out at very high light, where you have photoinhibition. Essentially, you're shining so much light on the phytoplankton, and the phytoplankton is not happy, and it shuts down its photosynthetic apparatus.

There's a whole series of theoretical/empirical curves for representing PI curves. One simple one that I like because it's fairly simple to conceptualize is that you have-- photosynthesis is going to be some function of  $P_{\text{max}}$ . There's some at high saturation. There's some  $P_{\text{max}}$  value that the cell will basically-- it has sufficient light, and that's as much photosynthesis as it can do.

And then you have, basically, a correction term for light, where if you look at this term, at very low light, if  $i$  goes to 0,  $e$  to the 0 goes to what?

**AUDIENCE:** 1.

**SCOTT DONEY:** Right  $1 - 1$ . So this goes to 0. So it has the correct behavior at low light. And if  $i$  goes to infinity,  $e$  to the minus infinity goes to 0. So this drops out, and you're left at  $P_{\text{max}}$ . So this does-- this saturating curve-- it doesn't do the photoinhibition part. You would have to add an additional term on for photoinhibition.

One little clever trick that I like is if you have an equation,  $e$  to the  $b$ , and if you look at the limit of that as  $b$  goes to 0,  $e$  to the  $b$  goes to  $1 + b$ . That's an approximation for the exponential.

The nice thing about that is if you look up at this term, that would say that the term  $e^{-\alpha z}$  would go to  $1 - \alpha z$ . And then the  $1s$  drop-- the  $1s$  drop out the  $\alpha z$ , because the  $P_{max}$ es also drop out. And so that's a way of thinking about what this  $\alpha$  term is, is it's actually the slope.  $\alpha$  is the slope of the  $P$  curve at low light. And sometimes you'll hear  $\alpha$  described as the initial slope.

So light is going to vary considerably over time, and it's going to vary for two reasons. Let's say we have our surface of the ocean, and we have depth. And we're going to plot time in this direction.

So if I were to look at the surface irradiance, you're going to get a seasonal cycle in most places outside the tropics. In the extra-tropics, you'll get a seasonal cycle where you'll have low light in the winter and high light in the summer, and then low light again in the winter. At the same time, mixed-layer depths tend to be deep in the winter and shallow in the summer and deep in the winter. So this would be-- that's  $z_0$ . This would be mixed-layer depth.

What the phytoplankton sees when it's in the mixed-layer depth, or in the mixed layer itself, is an average light over the mixed layer. The overturning time for mixed layers are on the timescales of 10s of minutes to maybe an hour, much shorter than the generation time for an individual phytoplankton. So these phytoplankton are getting caught up in turbulent eddies, and they're going up and down and up and down and up and down within the mixed layer.

And as an approximation, without going into a lot of details, you can say, well, they're seeing the average light of the mixed-layer depth. So when the mixed-layer depth is deep-- remember the light was dropping off exponentially? So when the mixed-layer depth is deep, even with the same surface irradiance, the average light experienced by the phytoplankton goes down. So during winter, you have lower effective light, both because you have lower light at the surface, and also you have lower light because of the deeper mixed layers.

Often, what you'll see in temperate latitudes is during the winter, if I were to plot on the same time axis and then I were to plot phytoplankton, what I would see is low phytoplankton in the summer, and then I might see some bloom event, and then it might collapse down, and then I might see another bloom event in the fall.

**AUDIENCE:** [INAUDIBLE]

**SCOTT DONEY:** Yeah. This is called the spring bloom. It's really original. And this is the fall bloom. This is not true everywhere, but it's canonical for, say, large parts of the temperate North Atlantic. The spring bloom is triggered by the fact that you have both rising surface light and shoaling mixed-layer depth, and you reach a point where you suddenly have enough light for the phytoplankton community to grow.

And there's a nice theoretical discussion of this that was originally put forward by Sverdrup. Just go to lecture 13. And it's called Sverdrup's critical light theory, or critical depth theory-- critical depth theory. And it goes something like this. At the surface, photosynthesis rates are high. And they tend to drop off with depth because of light. Let's assume for a moment that the phytoplankton is well-mixed, and we're just worrying about- we're just worried about the effect of light on photosynthesis. So this would be depth.

At some depth, you reach a depth- and we'll call this depth the compensation depth. The photosynthesis of the community is going to be balanced by the respiration. So this would be your community respiration.

So above this depth, the bugs are growing, and they're producing a lot more organic matter than is being consumed by the community. Below this depth, the phytoplankton just are not growing as fast as the respiration of the community. And so up here, you have net organic matter generation. Down here, you have net organic matter loss. And this  $C$  is called the compensation depth, compensation depth. And it's essentially where respiration compensates for photosynthesis.

Now, let's say this is all in a mixed layer. These are instantaneous photosynthesis rates, so this is the photosynthesis rate for that bug sitting there at that particular instance, at that depth. But if this is all in a mixed layer, the whole phytoplankton community is seeing this light-- the average light integrated over that depth-- we might want to know at what depth if we integrate the respiration,  $dz$ , would that equal the integrated photosynthesis?

And the argument there is that if the mixed layer is really deep and you have a lot of the community that's down in this region where you have net organic loss, you can't have a phytoplankton bloom. You'll have guys are growing up here, but then they get mixed down, and then they're down here starving, or they're being getting eaten, and they're just-- all of that organic matter can't go into new biomass and the phytoplankton can't bloom.

That depth is called a critical depth, where the total respiration integrated over the mix-- over this critical depth is equal to the total amount of photosynthesis. And you can solve for that if we assume that the-- if we assume for a moment that the irradiance will approximate as a surface irradiance and a single PAR.

Now, as I said, that's not a perfect assumption, but we'll go with it for right now because it makes the math very straightforward. We'll also assume that  $P$  scales linearly with  $I$ . So we're down in that linear part of the curve, so we have no saturation yet.

If you do that and you go back to these integrals,  $dr$ ,  $dz$  is just going to equal whatever your background canonical respiration. We're going to assume that that's constant with depth, times whatever this critical depth is. If it's constant and you integrate it, it's just that value times the depth.

The integral of  $pdz$  is then going to be the integral from 0 to  $z$  CR of  $\alpha$  times  $i$ , but  $i$  is then equal to  $i_0$ ,  $e$  to the minus  $kz$ ,  $dz$ . And that's going to equal-- did I do this right?  $\frac{1}{k}$ ,  $1 - e^{-kz}$  CR.

And so if you then set that equal, you can find a depth. You can solve for  $z$  CR, where the respiration and photosynthesis are equal. And the argument is that if  $z$  mixed layer is greater than  $z$  CR, then you get no bloom. But when mixed-layer depth is less than or equal to the critical depth, that's when you trigger a spring bloom.

And as long as you have some estimate of the respiration rate, the community respiration rate of the phytoplankton, you need to know the surface. If we go back up here-- you need to know the surface,  $P_0$ , or some idea of  $\alpha$ . Either will do. If you know  $\alpha$  and you know your irradiance and your background respiration, you can then compute the critical-- you can then compute the critical depth as a function of those parameters, and then you can compare it with your mixed-layer depth.

And so when the mixed-layer depth shoals, where we had that little the mixed-layer depth would go up like this, you'll reach a spot where-- let's say this was your  $z$  critical. You'll reach a spot where the mixed layer will shoal, and then you'll start to develop the bloom. And so then this all fills in with-- and you'll get this big spring bloom event.

We've run out of time, so we got through light. We'll start on Tuesday with nutrients, and we'll do nutrients, temperature, and DIC.