

# A COLLECTION OF RAMBLINGS ON TRADITIONAL AND NEW AVENUES OF PHYTOPLANKTON STUDIES AS THEY RELATE TO MARINE FOOD WEBS

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I suppose that in the beginning when research teams were organized to study plankton ecology a phytoplankton person was employed largely for two purposes. First, to identify the species of phytoplankton that were being collected, and secondly to measure primary production. The latter has always been thought of as perhaps a good thing in itself, and with some notable exceptions primary production has often been measured as a routine part of things. CalCOFI, until recently at least, has been an interesting exception.

Fortunately time passes and those of us who blindly measure primary production without knowing what really to do with the data are beginning to get the drift of some new directions, and I think that emphasis is shifting. This is in part because of the impact of theoretical ecologists telling us more about how natural systems work. In part it has something to do with the training of the people who are called upon to do the measurements, and there are lots of intangibles.

I learned rather late that one really ought to consider not only the production of plant material itself, but also what happens to it. What is the fate of phytoplankton production in the oceans? Those of us brought up in molecular biology traditions learned that one can write an equation for the growth of organisms in culture—a culture of bacteria or culture of unicellular algae, it's all the same. The differential equation says that the rate of change of the population is a function of the initial population times some growth constant. The ecologists would like us to be aware of the fact that there is also a mortality associated with the phytoplankton; and indeed if one is doing field work in an area he knows that phytoplankton crops go up and down or remain steady, but certainly there is no exponential increase year after year as would be predicted simply by the growth equation. Obviously, something happens to the stuff and we ought to think about that more.

The first question I'd like to address is, "What are the causes of phytoplankton mortality?" We know, at least over the long term, that if one subtracts mortality rates from growth rates the value approaches zero.

First of all it has long been known that phytoplankton sink, and in recent times there have been rather sophisticated measurements made of the rate at which phytoplankton sink. A number of generalizations have resulted from that sort of work. If a phytoplanktoner sinks out of the illuminated upper layer of the ocean it tends to consume itself by dark

respiration, or it may be eaten on the way down. If it reaches the bottom it enters a detrital food chain where it is probably eaten or decomposed by bacterial or fungal activity, in a way entirely analogous to a leaf fall in a forest. Phytoplankton no doubt do contribute to detrital food webs, probably more so in shallow coastal waters than offshore. But to my knowledge we have very little direct information on this point.

Those of you among the audience who are zoologists are aware that phytoplankton are eaten by herbivorous beasts. Much of the phytoplankton that is eaten, and the numbers vary from 20% to 30% or a bit more, is not digested but rather leaves the animal as fecal material. The fecal pellets of copepods sink too, and fecal pellet sinking rates have also been studied. Fecal pellets can either sink out of the water column and enter detrital food webs or it is conceivable, and probably likely, that many of them are eaten again on the way down as John Isaacs pointed out. The point is that not all phytoplankton production is immediately directed into a linear food web where it is grazed on only by herbivores.

Another point worth making is that not all the organisms that we commonly think of as phytoplankton are totally autotrophic. For example, in 1967 the Food Chain Group undertook a study of plankton populations off La Jolla. The study ran on for 7 months. Freda Reid and Jim Jordan laboriously counted all the phytoplankton taken in the weekly samples and discovered that about 5% of the phytoplankton biomass consisted of dinoflagellates that probably do not contain chlorophyll at all. The dynamics of this crop of nonchlorophyll-containing dinoflagellates was such that their numbers varied directly with the rest of the phytoplankton. This suggested to us that possibly they were feeding on phytoplankton directly, or else perhaps they utilized the dissolved organic matter released by the phytoplankton. To this day we don't know which alternative is more nearly correct because we haven't been able to get the organisms into culture in spite of several attempts.

Another role is the one Dick Dugdale brought out in his slide representing the model for nitrogen cycling: that phytoplankton play a rather direct role in nutrient recycling. Phytoplankton that are grazed upon and digested contribute their nutrients to the herbivore. The herbivore releases some of these with the excretory products. In case of nitrogen much of this is ammonia, a little bit is urea, some is organic nitrogen. Recent work has shown that ammonia and

urea can be directly reassimilated by phytoplankton. This recycling no doubt takes place at all stages of food conversion not only with the herbivores but with omnivores, carnivores, etc. Apparently most of the elements that we consider to be fertilizer elements, such as nitrogen, phosphorus, silicate, so forth, go through such cycles.

Dugdale has made a useful distinction between new production and regenerative production, where the regenerated production represents that based on recycled nutrients and new production representing inputs from the outside, whether it be nitrate upwelling from deep water, or nitrogen gas being fixed by blue-green algae in the water column, or what have you. The phytoplankton people have gotten into this aspect in some force recently.

Another role of phytoplankton has turned out to be to amuse modelers. In many civil engineering departments engineers have been called upon to prepare models of receiving waters of various kinds and to predict the behavior of phytoplankton in these waters. They have been relying heavily on Dugdale's nutrient uptake kinetics and on some of the generalizations about phytoplankton growth that have fallen out of other work. This has been very gratifying to the phytoplankton people because they almost began to feel useful for a change.

Geochemists and geologists are aware that phytoplankton contribute to the siliceous and carbonaceous sediments in the world's oceans. It's not clear to me, although it may be to others, whether this represents the sinking of phytoplankton directly from the water column, or whether most of their skeletons arrive via fecal material. But one suspects it's probably the latter. But to look at the role of the phytoplankton from the phytoplankton's "point of view," in the strictly evolutionary biologic sense, the role of the phytoplankton is to make more of themselves, and this they apparently do rather nicely. Almost all of the ecologically significant natural phytoplankton species apparently reproduce by simple cell division, one cell going to two. As Dick Dugdale pointed out, sex has been discovered in diatoms. Bob Holmes, when he was with the Food Chain Group, was aware of this. He saw gametes and auxospores in a variety of diatoms. But as yet we have no real way of identifying the importance of sexual reproductive activity in the maintenance of populations in the sea.

So much for the role of phytoplankton in marine food webs. I think I've said about all that I can say easily, and perhaps I should turn your attention to the role of the phytoplanktologist in understanding pelagic food webs.

I've already indicated that from simple beginnings a captive biologist can measure primary production and describe the species present. Some people have even broken out of that mold relatively early. For example, John Ryther wrote a rather classic paper in

*Science* in 1969, in which he considered the possibilities for fish production in various parts of the ocean. In that paper he assumed a strictly linear food web where one went from phytoplankton to herbivorous animals to carnivorous animals of several stages—there may be several of these—and he used a very simple mathematical expression to calculate the quantity of fish that could be produced. He noted that the production of fish would be equal to the production of phytoplankton times the efficiency of the food chain conversion in each trophic step to the  $n^{\text{th}}$  power where  $n$  represents the number of trophic levels or the number of steps in a linear food chain.

For clupeoid fisheries of upwelling regions,  $n$  was assumed to be 1.5, implying some feeding directly upon phytoplankton. For oceanic fisheries the number would be larger, 3 to 5, as one plays games with this kind of an equation. You can make some pretty good guesses about what phytoplankton production is, but then one stumbles over what are the efficiencies of utilization. This point came up in Professor Isaacs' talk this morning in reference to the value of  $n$ . I agree with Professor Isaacs that  $n$  is probably not some simple integer like 2, 3, or 4.

What needs to be represented is that food chains are not linear and that the young of a carnivore may be herbivorous, that considerable cycling of energy may take place among the smallest size classes of planktonic organisms, that wastes may be eaten or absorbed, to related complexities. Certainly, the consumption of gametes, for example, mixes up the food web, as does cannibalism. True herbivory may be limited to laboratory cultures.

It is clear from the way that the fisheries scientists go about their work that it isn't just fish in general, or phytoplankton production in general, or copepod production in general that is interesting and useful, but rather the production of particular species. So I think it's time that the primary production field faced up to the need for understanding food webs at the species level, and this is the point that I would like to emphasize with a couple of examples.

Off of Southern California we occasionally have red tides. These are blooms of the phytoplankton that involve not more than a dozen species of dinoflagellates and usually one or two species are predominate, most frequently *Gonyaulax polyedra*, *Prorocentrum micans*, one of the *Ceratium* species, or *Gymnodium splendens*. One of the questions that one can ask is: Why do these species bloom and not diatoms?

To give a conception of the relative magnitude of things, a burst of upwelling off La Jolla can lead to either a bloom of diatoms or a bloom of dinoflagellates. If we get a bloom of diatoms, and we are measuring the standing stock of phytoplankton as chlorophyll, we rarely see chlorophyll levels more than about 15  $\mu\text{g}/\text{l}$ . On the other hand in the

dinoflagellate blooms, if we take a sample at the surface in mid-afternoon, we can see as much as 300  $\mu\text{g/l}$  of chlorophyll. What's going on? It has been known for a long time that these red tide dinoflagellates can undertake diurnal-vertical migrations and that they aggregate at the surface in the daytime, particularly from midday to mid-afternoon. This apparently accounts for the high concentration of chlorophyll and of cells that we see. The dinoflagellates can take advantage of nutrients in the upper 15 m or so of the water column whereas a diatom, with no independent locomotion of its own, is restricted to getting nutrients that are in the parcel of water immediate adjacent to it. So it is obvious that these vertically migrating dinoflagellates have a physiological idiosyncrasy in their vertical migration that allows them to sweep nutrients out of a rather larger parcel of water than diatoms can do. Dr. Lasker is going to talk about this in more detail tomorrow but it's of such significance in my view of the world that I'd like to mention it now.

He's been studying the feeding abilities of larval anchovies and finds that they will feed on certain of the dinoflagellates that are common in red tides. The physical size of the cell is apparently just right for the first feeding anchovy larvae and furthermore the aggregation abilities of these species allow high enough concentrations for the fish larvae to full their guts. It looks to me as if the idiosyncrasies of dinoflagellates in this regard may be of interest not only to phytoplankton people but to those concerned with the anchovy food web. I certainly hope it works out that way.

This brings up another point that I'd like to make (in leaving the flat earth society and joining the round earth society): that phytoplankton people can hope to interact more with people concerned with organisms at other trophic levels. Another peculiar set of phytoplankters that appear to be important in a particular food web is that of chain diatoms in the anchoveta food web in the Peru current. I'm told by Sra. Blanca Rojas de Mendiola, who studied the gut contents of the anchoveta in Peru, that the gut contents of the anchoveta over much of the year consists largely of the remains of diatoms and most of these are chain diatoms that form rather large particles. It is apparently these relatively large phytoplankton species that are of special interest. If one takes a water sample and counts all the phytoplankton in it, he finds that there is always a background of rather small celled phytoplankters and that numbers are variable for the chain diatoms. We need to know about the mechanisms that regulate the size and species composition of phytoplankton crops and why we see so much switching about of the dominant forms.

These two examples point out some idiosyncrasies among phytoplankton that make certain species or groups of species of particular interest to rather specific food webs. In the case of the chain diatoms,

their desirability seems to be based entirely on their size; at least we have no information beyond this. It's possible that their lipid composition or something else might also contribute. But it would appear that phytoplankton people could profitably amuse themselves by trying to collect information on physiological responses of some of these ecologically important species, and in fact this has been going on for years.

Earlier Curl and McLeod published a paper on *Skeletonema costatum*, a chain diatom, where they measured growth as functions of light, temperature and salinity. Braarud in Norway had been doing that even in the 40's. So there's a rather strong tradition in this area. I'm sure there must be other examples of this sort where the problem is not the overall production of phytoplankton but rather the production and success of either single species or small groups of species.

If one takes as his goal, at least for the purposes of this symposium, understanding something about marine food webs, then he is interested in the regulation of the population sizes and of the growth success of these rather discrete groups of phytoplankton. He should also be interested in their biogeographic distributions at the species level. There is a lot of work going on to examine, or to try to explain from laboratory studies with culture, why certain species of phytoplankton occur where they do, and why they are more abundant at one season of the year than the other. In this context I would like to mention that Ted Smayda at the University of Rhode Island and Bill Thomas in an analogous study of the eastern tropical Pacific, have been laboriously going through the dozen or so ecologically significant species in Narragansett Bay, collecting information on growth rate as a function of temperature, light, day length, and almost every other possible variable, trying to figure out why species X is abundant in January and February and species Y is abundant in March and April. This rather laborious kind of work, I think, has a future.

There is another area in which phytoplankton folks are contributing. Until now the contributions are related to the engineering models that I mentioned earlier. But it has been possible after 20 years of culturing things in the laboratory to draw some generalizations about the growth behavior of phytoplankton which allow one to make some rather sophisticated expectations as to how growth rate would vary as a function of temperature, light, and cell size, aspects such as Dick Dugdale showed in his slide for nitrate uptake versus light intensity, nutrient uptake versus concentration, and so forth. I should tell you what the list of these generalizations, so far conceived, consists of. First, there are the nutrient kinetics models and generalizations. Second, it has been found that sinking rate is a predictable function of the size of cells. Third, there is a rough relationship between the maximum

growth rate of the phytoplankton cell and its size. This maximum growth rate is that observed in cultures where the phytoplankton are hopefully growing under nearly optimal conditions. So far most of these generalizations are based upon size, and since size is of interest as far as feeding is concerned, then I think that perhaps they are useful.

In a recent paper Tim Parsons and Mac Takahashi wrote some equations taking into account these generalities in order to come up with some predictions as to what kinds of phytoplankters would be most successful in different oceanic environments, such as open ocean, coastal-temperate, coastal-tropical, and so forth. We seem to be getting to the point where we can make reasonable guesses as to what kinds of phytoplankters might be most successful in particular places. So these generalizations on phytoplankton behavior I think are a good thing and I know that they are of some use now to mathematical models of plankton production. I hope that they will become more useful as, first of all, they get "debugged" a bit and as people become more aware of them.

There is another role for phytoplanktologists that is a little bit different and more traditional, along the lines of investigating metabolic processes that are of ecological significance. Dick Dugdale mentioned one this morning, the repression by ammonia of the assimilation of nitrate. It seems to be a general phenomenon. There may be some peculiar idiosyncrasies in that area, as among the red tide dinoflagellates. We're going to have a look and see, but, for all practical purposes, this seems to be a universal thing of some usefulness if one is concerned with phytoplankton growth about sewage outfalls or other highly eutrophic waters.

Some other metabolic processes are not so well known but may influence overall production. There is a phenomenon studied most among higher plants called photo-respiration. It has been discovered that most crop plants, such as wheat, waste much of their photosynthetic energy at high light intensities. They fix carbon but instead of it going through the Calvin cycle and coming out as sugars and starch food reserves, some of the carbon is shunted off as glycolic acid. Since the energy in the carbon-to-carbon bonds is not conserved in that pathway, it appears to be a hopelessly wasteful phenomenon. We would like to know if that sort of thing goes on in the ocean. Efforts are underway to see whether phytoplankton grown in a laboratory show this photo-respiration and to determine whether it is important in the ocean. I should note that among higher plants there are some significant crop plants that do not have photo-respiration, and they are more productive than the ones that do have it. For example, corn and sugar cane do not have photo-respiration and the maximum yield per acre for those two crop plants

exceeds that of wheat, rye, and tobacco that show photo-respiration.

Another phenomenon at the physiological level of investigation concerns the inhibition of photosynthesis, and as you saw this morning, nitrate-uptake at high light intensities. If one plots photosynthesis as a function of depth, most of the graphs show a suboptimal rate at the sea surface. This may seem to be a trivial problem but I suppose as much as 10 or 20% of primary production is "on the line" depending on whether you think the effect is valid or that it is an artifact.

A number of people think it is an artifact of putting things in bottles. Phytoplankters held in bottles at the sea surface can no longer participate in the wave-induced, Langmuir circulation that would normally expose them to a range of light intensities. Being held in continuous bright light is somewhat unnatural. Other people think that it is a real effect related to the ultraviolet portion of the electromagnetic spectrum and that there is UV inhibition of photosynthesis. We'll find out in a year or so when people start publishing their results.

Another metabolic process of considerable interest is the fixation of nitrogen. As you know, N-fixation is significant among bacteria that form nodules on the roots of legumes, alder trees, and so forth. So far only a very few species of phytoplankton have been identified from the ocean that can fix nitrogen and these are blue-green algae. One of them, *Trichodesmium*, has been known for a long time, and Dugdale and Goering did the pioneering study of its N-fixation in the Sargasso Sea. Another N-fixing blue-green algae that Tim Mague in the Food Chain Group and Venrick have been studying in the Pacific is an intracellular endosymbiont called *Richelia* which occurs inside the cells of the diatom *Rhizosolenia*. Inasmuch as this nitrogen fixation is a source of new production and doesn't represent just the recycling of what nitrogen is already there, it is a significant and important phenomenon. Mague tried to estimate how much nitrogen fixation went on in the central Pacific compared with the assimilation of recycled ammonia and urea and he found that it was perhaps 10 or 20% of the total nitrogen turnover in the summertime. It is my understanding that this nitrogen fixation is limited in the summertime.

The approaches that appear interesting at the moment for extending our knowledge are first of all to turn away from the concept of linear food webs and to start paying more attention to individual species and groups of species. So far this looks interesting in terms of size categories of phytoplankton, separating phytoplankton into size groups, large ones, small ones, and so forth. For dinoflagellates not only size appears to be important in their blooms but their vertical migration behavior also seems to be of ecological significance since this

leads to aggregations of cells in sufficient concentrations for successful grazing of animals.

People have recognized for years that there is a general relation between the production of fish in an area and the primary production or the nutrient input rate. We know that the coastal Peru fishery, except during El Niño years, is characterized by high rate of nutrient input, high phytoplankton stocks, and high production of fish. We know that in the middle of the Pacific the converse is true.

Bill Sutcliffe at the Bedford Institute has sent me some reprints that are rather speculative attempts to show that this kind of comparison or this kind of phenomenon might be more important in fisheries where it's never really been looked at before, and I can tell you briefly what he's done. He has taken data on the flow of the St. Lawrence River over the years and by proper statistical fudges, averaging 3 year means and so forth, he finds that there is a

relationship between the flow of the St. Lawrence and the catch of some of the New England commercial fisheries, lobster and some others. I'm certainly not qualified to determine whether these statistical correlations that he has are viable and will stand the test of time, but they're pretty interesting. His argument is that the greater the river flow, the more of the underlying, nutrient-rich water is entrained in the flowing fresh water carried out to sea. The nutrient input to the coastal waters off northern New England would then be almost directly related to the river flow. Of course he must lag the lobster catch 4 or 5 years after this nutrient input related to river flow to account for the time it takes for the lobster to grow to commercial size. The implication is, if this lag is justified, that the survival of the larvae and juveniles is closely tied to nutrient input.