Phytoplankton Growth – Literature for the basics

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The phytoplankton are the base of virtually all food webs in the oceans, lakes and seas on Earth. If you like they can be compared to the vegetation on land, and just like land based plants the phytoplankton need light and nutrients to grow. Unlike most terrestrial vegetation, the phytoplankton are not plants but rather algae, and some groups of bacteria that are able to photosynthesize. Seaweeds are also algae (macro-algae) whereas the phytoplankton are microalgae due to the fact that they are mostly single cells and can only be seen with the aide of a microscope. The analogy with terrestrial plants falls down a bit since, although phytoplankton need water, naturally since they are surrounded by the stuff it is hardly in short supply! Also, the nutrients they need for growth are contained in the water bathing the cells and so the whole basis of nutrient uptake, and gas exchange is based on diffusion gradients between the inside of the cell and concentrations in the surrounding seawater.

Naturally there has been much written on the phytoplankton and how they grow. Although a little dated the review by Fogg (1991) is a superb introduction the the *phytoplankton way of life*. In it the eloquently addresses the key limitation factors to growth, light, nutrients and importantly the key role that the ocean currents and wind driven movements of surface waters play in controlling phytoplankton dynamics. It is important to always bare in mind that the phytoplankton cannot swim against the movement of water masses, and so the physics (e.g. light penetration, temperature, density, boundary layer effects with other water masses) of the system, be it an ocean, lake, farmyard pond really does determine the ability of algal populations to grow. One of the most comprehensive texts covering, the basics of photosynthesis, algal growth and both large-scale (ocean & lake) processes to small-scale (boundary layer effects at individual cell surfaces) is that of Williams et al. (2002). This is superbly complemented by Falkowski & Raven (2007). At a more non-specialist level chapters 2 & 3 of Kaiser et al. (2011) cover the main issues regarding the controlling factors of phytoplankton growth and seasonal dynamics

Falkowski, P. G. & Raven, J. A. 2007. Aquatic Photosynthesis 2nd Edition. Princeton University Press.

Fogg, G. E. 1991. Tansley Review No. 30. The phytoplankton ways of life. New Phytologist, 118, 191–232.

Williams, P. J. le B., Thomas, D. N. & Reynolds, C. S. 2002. Phytoplankton Productivity: Carbon Assimilation in Marine and Freshwater Ecosystems. Wiley Blackwell.

Kaiser, M.J., Attrill, M., Jennings, S., Thomas, D.N., Barnes,D., Brierley, A.S., Hiddink, J.G., Kaartokallio, H., Polunin, N & Raffaelli, D. 2011. Marine Ecology - Processes, Systems and Impacts. 2nd Edition. Oxford University Press.

Ultimately the factors key controlling phytoplankton growth are light (both quality and quantity), nutrient availability (gases, and inorganic nutrients). The fact that phytoplankton are found from tropical waters through to the polar oceans (albeit different species) are indicative that temperature is not itself a key limiting factor to growth, at least in general terms. Below is a selection of publications that should give a good start for unravelling the complexity of how it is possible for phytoplankton growth to occur. This growth can be dramatic with crystal clear waters being transformed in to murky brown, green or even red (depending on the species of phytoplankton involved) in the matter of a few hours when all the nutrient and light conditions are perfect for growth. It is still a wonder that in such a small space of time the microscopic (single cells) can become the macroscopic visible from space (blooms covering 100s and 1000s km^2).

Light

Ultimately light is arguably the key factor determining phytoplankton growth, since without light there can be no photosynthesis (although with no CO_2 or O_2, there cannot be photosynthesis either). Many factors interact to influence the transmission of light to depth ranging from the absorption properties of the water itself through to the scattering of light by bubbles and particles suspended in the water. Even the phytoplankton themselves alter the transmission of light. Whereas in clear polar or tropical waters light can still be measured around 250 metres and algae have been growing at such depths, in a turbid, sediment laden estuary light may just penetrate just a few metres or even less. The definitive work describing all aspects of light in aquatic systems is Kirk (2010). It is important to remember that only a small part of the light spectrum (photosynthetic active radiation, PAR) is absorbed by chlorophyll and other pigments contained in algae, and so it is not only the total amount of light reaching depth, but also the spectral quality of the light.

Kirk J.T.O. 2010. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press.

Nutrients

Photosynthesis and respiration are of course the key to harnessing sunlight and producing energy to drive metabolism (autotrophy), however, a host of other nutrients such as nitrogen, phosphorus, silicate, sulphur are needed to form proteins, nucleic acids, carbohydrates and lipids that go into making a viable organism. In fact the list of chemical ingredients that make up a living cell is huge and includes metals needed in trace amounts such as iron, cobalt and zinc. In most aquatic systems one or several nutrients are limited in supply or are quickly used up when algal growth gets underway (Arrigo, 2005; Sarmiento & Gruber 2006). Without re-supply no further growth is possible. So for instance there can be loads of nitrogen or phosphorus available (and plenty of light), but if iron is missing (even though it is needed in just trace amounts) algae will not grow. A good example of this is in the Southern Ocean where experiments have shown that by adding iron to iron-poor waters can stimulate phytoplankton growth. See Boyd et al. (2007) for a comprehensive review of this and the possible consequences for whole ocean ecosystems Smetacek and Nicol (2005).

Arrigo, K. R. 2005. Marine microorganisms and global nutrient cycles. Nature, 437, 349–355.

Boyd, P. W. and 22 others. 2007. Mesoscale iron enrichment experiments 1993–2005: Synthesis and future directions. Science, 315, 612–617.

Sarmiento, J.L. & Gruber, N. 2006. Ocean Biogeochemical Dynamics. Princeton University Press.

Smetacek, V. and Nicol S. 2005. Polar ocean ecosystems in a changing world. Nature, 437,362–368.

Gases

Naturally, CO_2 and O_2 are vital for photosynthesis (consumes CO_2 and produces O_2) and respiration (consumes O_2 and produces CO_2)to take place. Fortunately there is plenty of both these gases in the oceans and they are rarely limiting (Broecker 2003). However, a key issue of global importance is the measured changes in CO2 content of seawater and the associated gradual lowering of ocean pH, commonly referred to as *ocean acidification*. Since the industrial revolution in the 1700s it is estimated that the oceans have dropped in pH by about 0.1 pH unit and it is predicted that by 2100 the worlds oceans may have undergone a further decrease of about 0.4 pH units (Zeebe et al. 2009). This change in pH is predicted to have considerable effects on many biological processes in the ocean, and especially organisms that use calcium carbonate in their skeleton or external shells (Raven et al., 2005; Fabry et al. 2008).

Broecker, W. 2009. Wally's quest to understand the oceans $CaCO_3$ cycle. Annual Review of Marine Science, 1, 1-18.

Fabry, V.J., Seibel, B.A., Feely, R.A. & Orr, J.C. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. ICES of Marine Science, 65, 414-432.

Raven, J., Caldeira, K., Elderfield, H., Hoegh-Guldberg, O., Liss, P., Riebesell, U., Shepard, J., Turley, C. & Watson, A. 2005. Ocean acidification due to increasing atmospheric carbon dioxide. Royal Society of London, Policy Document 12/05. 68pp.

Zeebe, R.E., Zachos, J.C. Caldeira, K. & Tyrrell, T. Carbon emissions and acidification. Science, 321, 51- 52.

Formation of blooms

The onset of phytoplankton blooms is initiated when there is enough light to saturate the photosynthetic process and enough nutrients to support the production of new cell material allowing growth and cell division (most phytoplankton population growth is by simple cell division). It is important to remember that phytoplankton are not stationary at the surface of the ocean (highest light regime), but constantly being mixed by water movement through the surface of the water column. Whether a population of phytoplankton get enough light for net growth is an interplay between the depth of mixing and the transmission of light through the water (as well as nutrient supply). This has led to the development of the *critical depth theory*, which is central to our interpretation of seasonal phytoplankton blooms in temperate oceans and seas. This is discussed by Sverdrup (1953), Smetack and Passow (1990), Siegel et al (2002) although the ideas presented by Bahrenfeld (2010) need to be considered.

Behrenfeld, M. J. 2010. "Abandoning Sverdrup's Critical Depth Hypothesis on Phytoplankton blooms". Ecological Society of America, 91, 997-989.

Siegel, D.A. Doney, S.C. and Yoder, J.A. (2002). The North Atlantic spring phytoplankton bloom and Sverdrup's critical depth hypothesis. Science, 296, 730-733.

Smetacek, V., & Passow, U. (1990) Spring bloom initiation and Sverdrup's critical-depth model. Limnology and Oceanography, 35, 228-234.

Sverdrup, H. U. (1953) On conditions for the vernal blooming of phytoplankton. J. Cons. Perm. Int. Exp., 18, 237-295.

Measuring algae from space

The most revolutionary of changes in biological oceanography over the past thirty years has been the deployment of satellite and aircraft-borne sensors that can record the colour of water masses. These give us the means to looking at the large-scale distribution of phytoplankton so that monthly and annual and inter-annual distribution patterns can be created (McClain, 2009).

McClain, C.R. 2009. A decade of satellite ocean color observations. Annual Review of Marine Science, 1, 19-42.

Paradox of the plankton

In conclusion it is worth considering the so called *Paradox of the Plankton*: that is when resources are limited and species are having to compete for them in a homogenous media normally a single species will dominate. However, in the plankton, despite the limited resources, there are many species co-existing, an apparent ecological paradox? The concept was introduced by Hutchinson in 1961 and has been subsequently debated long and hard by general ecologists and biological oceanographers. A comprehensive summary of this debate is given by Rohde (2006). In a similar vain, when considering the complex issues of phytoplankton ecology it is also worth taking a look at the mini-essays of Smetacek (1999, 2001 & 2002) who gives great insight into the complexity of different groups and the history of the study of phytoplankton competing for limited resources.

Hutchinson, G.E. 1961. The paradox of the plankton. American Naturalist, 95, 137–145.

Rohde, J. 2006. Nonequilibrium Ecology. Cambridge University Press.

Smetacek, V. 2002. The ocean's veil. Nature, 419, 565.

Smetacek, V. 2001. A watery arms race. Nature, 411, 745.

Smetacek, V. 1999. Revolution in the ocean. Nature, 401, 647.