Primary Production: From Inorganic to Organic Carbon

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Primary production involves the formation of organic matter from inorganic carbon and nutrients. This requires external energy to provide the four electrons needed to reduce the carbon valence from four plus in inorganic carbon to near zero valence in organic matter. This energy can come from light or the oxidation of reduced compounds, and we use the terms photoautotrophy and chemo(litho)autotrophy, respectively. Total terrestrial and oceanic net primary production are each $\sim 50\text{--}55 \text{ Pg yr}^{-1}$ ($1 \text{ Pg} = 1 \text{ Gt} = 10^{15} \text{ g}$; Field et al. 1998). Within the ocean, carbon fixation by oceanic phytoplankton ($\sim 47 \text{ Pg yr}^{-1}$) dominates over that by coastal phytoplankton ($\sim 6.5 \text{ Pg yr}^{-1}$; Dunne et al. 2007), benthic algae ($\sim 0.32 \text{ Pg yr}^{-1}$; Gattuso et al. 2006), marine macrophytes ($\sim 1 \text{ Pg yr}^{-1}$; Smith 1981) and chemo(litho)autotrophs (~ 0.4 and $\sim 0.37 \text{ Pg yr}^{-1}$ in the water column and sediments, respectively; Middelburg 2011). Much of the chemolithoautotrophy is based on energy from organic matter recycling. Since, photosynthesis by far dominates inorganic to organic carbon transfers, we will restrict this chapter to light driven primary production.

Gross primary production refers to total carbon fixation/oxygen production, while net production refers to growth of primary producers and is lessened by respiration of the primary producer. Net primary production is available for growth and metabolic costs of heterotrophs, and it is the process most relevant for biogeochemists and chemical oceanographers. For the time being, we present primary production as the formation of carbohydrates (CH_2O) and ignore any complexities related to the formation of proteins, membranes and other cellular components (Chap. 6), because these require additional elements (nutrients). The overall photosynthetic reaction is:

It starts with the absorption of light energy by photosystem II (PSII):

This reaction yields energy to generate adenosine triphosphate (ATP). The oxygen produced originates from the water and can be considered a waste product of photosynthesis. The protons and electrons generated subsequently react with nicotinamide adenine dinucleotide phosphate (NADP⁺) at photosystem I (PSI):

The energies of NADPH and ATP are then used to fix and reduce CO₂ to form carbohydrate.

This reaction is normally mediated by the enzyme ribulose bis-phosphate carboxylase (RuBisCO).

Primary production is at the base of all life on earth; it is thus important to quantify it and to understand the governing factors. We will first present, at a very basic level, the primary producers. This will be followed by the introduction of the master equation of primary production, based on laboratory studies, and then a discussion of its application to natural systems.

2.1 Primary Producers

Primary producers in the ocean vary from µm-sized phytoplankton to m-sized mangrove trees. Phytoplankton refers to photoautotrophs in the water that are transported with the currents (although they may be slowly settling). Biological oceanographers usually divide plankton (all organisms in the water that go with the current) into size classes (Table 2.1). Most phytoplankton are in the pico, nano and microplankton range (0.2–200 µm). The prefixes pico and nano have little to do with their usual meaning in physics and chemistry. Their small size gives them a high-surface-area-to-volume ratio which is highly favourable for taking up nutrients from a dilute solution. Within these phytoplankton size classes there is high diversity in terms of species composition and ecological functioning. Both small cyanobacteria (*Synechococcus* and *Prochlorococcus*) and very small eukaryotes (e.g., Chlorophytes) contribute to the picoplankton. Microflagellates from various phytoplankton groups (Chlorophytes, Cryptophytes, Diatoms, Haptophytes) dominate the nanoplankton and differ in many aspects (cell wall, nutrient stoichiometry,

Table 2.1 Plankton size classes in the ocean

Size lass	Name (example)
<0.2 μm	Femtoplankton (virus)
0.2–2 μm	Picoplankton (bacteria, very small eukaryotes)
2–20 μm	Nanoplankton (diatoms, dinoflagellates, protozoa)
20–200 μm	Microplankton (diatoms, dinoflagellates, protozoa)
0.2–20 mm	Mesoplankton (zooplankton)
2–20 cm	Macroplankton

pigments, number of flagellae, life history, presence/absence of frustule). While phytoplankton communities can be described in terms of species, size classes or molecular biology data based partitioning units, they can also be divided into different functional types (diatoms because of Si skeleton, coccoliths with CaCO_3 skeleton, N_2 -fixers, etc.). Unfortunately, taxonomic, functional and size partitionings among phytoplankton groups are not necessarily consistent.

A substantial fraction of the ocean floor in the coastal domain receives enough light energy to sustain growth of photoautotrophs. This includes not only intertidal areas, but also the subtidal. Small-sized photoautotrophs (microphytobenthos, including diatoms and cyanobacteria) are again the dominant primary producers, but macroalgae, seagrass, saltmarsh plants and mangrove trees contribute as well. Seagrasses, saltmarsh macrophytes and mangrove trees have structural components and specialised organs (roots and rhizomes) to tap into nutrient resources within the sediments.

2.2 The Basics (For Individuals and Populations)

Carbon fixation by (and growth of) primary producers will be discussed based on the master equation of Soetaert and Herman (2009):

$$P = \mu \cdot B \cdot f_{\text{lim}}(\text{resources, conditions}) \quad (2.1)$$

This master equation simply states that production (P , mol/g per unit volume per unit time) is proportional to the biomass (B , mol/g per unit volume) of the primary producer, the actor, which has an intrinsic maximum growth rate of μ (time^{-1}) and is limited ($0 < f_{\text{lim}} < 1$) by either physical conditions (e.g., temperature, turbulence) or resources such as light, nutrients and dissolved inorganic carbon. This equation is simple and generic, and we will show below how it relates to phytoplankton global primary production estimates using remote sensing, to expressions used in numerical biogeochemical models and to exponential growth in the laboratory.

2.2.1 Maximum Growth Rate (μ)

Consider a primary producer in an experiment supplied with all the resources it needs and under ideal conditions, in other words the limitation function f_{lim} is equal to one and optimal growth occurs. Equation 2.1 then reduces to the change in B with time, or production P, is equal to $\mu \cdot B$:

$$P = \frac{dB}{dt} = \mu B \quad (2.2)$$

This is the well-known equation for exponential growth:

$$B = B_0 e^{\mu t}, \text{ or alternatively : } \mu = \frac{1}{t} \ln \frac{B}{B_0} \quad (2.3)$$

where B is the biomass at times t and B_0 is the initial biomass. Plotting the logarithm of biomass development as function of time yields then a slope corresponding to μ . Sometimes data are reported as the number of cell divisions (or doublings) per day: $\mu_d = \frac{1}{t} \log_2 \frac{B}{B_0}$.

Maximum growths for phytoplankton typically varies from 0.1 to 4 d^{-1} , implying doubling times $\left(\frac{\ln 2}{\mu}\right)$ of a fraction of a day to one week. Figure 2.1a shows a typical example of exponential growth for maximum growth rates of 0.1 to 2 d^{-1} . Exponential growth leads to rapid depletion of substrates and after some time, resources become limiting and phytoplankton enters into a stationary phase (Fig. 2.1b). Maximum growth size depends on phytoplankton group and size (Fig. 2.2; Box 2.1).

Fig. 2.1 **a** The increase in biomass during exponential growth with growth rates of 0.1, 0.5, 1 and 2 d^{-1} . **b** Cell growth of the diatom *Thalassiosira pseudonana* is exponential (growth rate of 1.4 d^{-1}) till nitrate is depleted and then stationary growth occurs (Data from Davidson et al. 1999)

Fig. 2.2 **a** The relationship between growth rate and phytoplankton cell size and model prediction (grey curve) (Ward et al. 2017). **b** The relationship between growth rate and phytoplankton cell size (solid black line). Maximum nutrient uptake and requirement per cell scale positively with cell size (dashed blue line), while theoretical maximum growth rates scale negatively (solid blue line)

2.2.2 Temperature Effect on Primary Production

The temperature of a system provides a strong control on the functioning of organisms. Growth responses of populations to temperature are usually expressed by thermal tolerance curves, also known as reaction norms. Starting at low temperatures, growth initially increases linearly or exponentially up to a maximum T_{opt} and then typically declines relatively more rapidly: i.e. the response curve is often skewed to the left. In other words, phytoplankton growing near its optimum temperature is more sensitive to warming than to cooling (Fig. 2.3).

Although populations show distinct unimodal responses to temperature, mixed communities, and thus ecosystems, usually exhibit a smooth, monotonical increase best described by an exponential ($\mu = ae^{bT}$, Fig. 2.4). The thermal response can then be described by

$$\mu = ae^{bT} \left[1 - \left(\frac{T - T_{opt}}{width/2} \right)^2 \right] \quad (2.4)$$

where a and b are empirical parameters describing the maximum envelope for the mixed community and T_{opt} and $width$ describe the maximum growth rate and temperature range of individual populations. Eppley's (1972) seminal work on temperature and phytoplankton growth in the sea reported values of 0.59 for a and 0.0633 for b . Note that this community response provides an upper limit for individual species and that high growth rates for individual species trade off with

Fig. 2.3 Temperature response of the specific growth rates of three eukaryotic phytoplankton classes (Diatoms, Dinoflagellates, Chlorophytes) and of Cyanobacteria from temperate freshwater and brackish environments (modified from Paerl et al. 2011). *A. form* = *Asterionella Formosa*, *T. rot* = *Thalassiosira rotula*, *P. tric* = *Phaeodactylum tricornutum*, *H. triq* = *Heterocapsa triquetra*, *P. min* = *Prorocentrum minimum*, *C. furc* = *Ceratium furcoides*, *G. rad* = *Golenkinia radiata*, *Chlor. sp.* = *Chlorella sp.*, *S. cing* = *Staurastrum cingulum*, *A. ucr* = *Anabaena ucrainica*, *M. aer* = *Microcystis aeruginosa*, *A. flos* = *Aphanizomenon flos-aquae*, *C. sperm* = *Cylindrospermopsis raciborskii*

growth rates at other temperatures, with the consequence that species replace each other (Fig. 2.4).

This exponential temperature response of natural communities is usually expressed in terms of Q_{10} values or Activation energies E_a , both rooted in chemical thermodynamics (van 't Hoff and Arrhenius equations). The temperature Q_{10} is normally defined as

Fig. 2.4 Phytoplankton growth rate (d^{-1}) for a mixed community comprised of polar, temperate and tropical species. The mixed community response is based on Eppley (1972)

$$Q_{10} = \left(\frac{\mu_T}{\mu_{Ref}} \right) e^{\left[\frac{10}{(T - T_{Ref})} \right]} \quad (2.5)$$

where μ_T and μ_{Ref} are the rate (e.g. growth) at temperature T and the reference temperature T_{Ref} (Celsius). Q_{10} can be simplified to

$$Q_{10} = \left(\frac{\mu_{Ref + 10}}{\mu_{Ref}} \right) \quad (2.6)$$

because it gives the rate increases for a 10 °C increase in T and is related to the parameter b of the exponential increase: $Q_{10} = e^{10b}$. Eppley's curve thus

corresponds to a Q_{10} of 1.88. Typical Q_{10} values for biological processes are between 2 and 3.

The Arrhenius equation is very similar and reads

$$\mu = Ae^{\frac{-E_a}{RT}} \quad (2.7)$$

where A is a pre-exponential factor (time^{-1}), E_a is the activation energy (J mol^{-1}), R is the universal gas constant ($8.314 \text{ J mol}^{-1} \text{ K}^{-1}$) and T is the absolute temperature (K). Sometimes the universal gas constant R is replaced by the Boltzman constant k ($8.617 \cdot 10^{-5} \text{ eV K}^{-1}$) and then E_a is expressed in eV (energy per molecule) rather than J mol^{-1} . For the temperature range of seawater, E_a and Q_{10} values are related via

$$E_a = \frac{-R \ln Q_{10}}{\left(\frac{1}{T} - \frac{1}{T_{\text{Ref}}}\right)} \text{ and } Q_{10} = e^{\left[\left(\frac{E_a}{R}\right) \frac{10}{(T - T_{\text{Ref}})}\right]}, \quad (2.8)$$

where T is again given in degrees Kelvin. Eppley's Q_{10} of 1.88 corresponds to activation energies of about 0.47 eV or 45 kJ mol^{-1} at 20°C . One should realize that this is the optimal community temperature response, i.e. no other limiting factors. Apparent activation energies and Q_{10} values in the ocean are $\sim 0.30 \text{ eV}$ (29 kJ mol^{-1}) and ~ 1.5 , respectively, close to that of Rubisco (Edwards et al. 2016).

2.2.3 Light

Photosynthesis is a light dependent reaction, and light intensity has a major impact on growth rates. The relationship between photosynthesis and irradiance is normally presented as a P versus E curve, where E refers to radiant energy ($\text{mol quanta m}^{-2} \text{ s}^{-1}$). Multiple equations have been presented to represent the photosynthesis to light relation, which differ in the number of parameters and whether or not they include the photo-inhibition effect at high light intensities or respiration of the autotroph. Photorespiration, the breakdown of photo-labile, intermediate carbon fixation products, is important in full-light exposed organisms, such as terrestrial plants, microphytobenthos and phytoplankton in the surface layer.

Common simple limitation functions are the hyperbolic, Monod model:

$$f_{\text{lim}}(E) = \frac{E}{(E + K_E)} \quad (2.9)$$

where $f_{\text{lim}}(E)$ is the light limitation function ($0 < f_{\text{lim}}(E) < 1$), K_E is a light-saturation parameter (typically $50\text{--}150 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ for marine phytoplankton), and the Steele model (1962):

$$f_{lim}(E) = \frac{E}{E_{max}} e^{\left(1 - \frac{E}{E_{Max}}\right)} \tag{2.10}$$

where E_{max} is typically 50–300 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ for marine phytoplankton (Soetaert and Herman 2009). The Steele model represents both the initial increase and the subsequent decrease due to photo-inhibition with only one parameter (Fig. 2.5).

Fig. 2.5 Example of light inhibition functions in use. The Web and Monod models do not have light inhibition and only show different saturation behaviours, while the Steele and Platt models do incorporate the decrease in phytoplankton growth at high light levels, due to photo-inhibition

The Webb et al. (1974) model is based on an exponential:

$$f_{lim}(E) = 1 - \left[1 - e^{\left(\frac{\alpha E}{P_{max}}\right)} \right] \quad (2.11)$$

where P_{max} is the maximum rate at high light and α is the initial slope (increase in P with E at low light intensity). This equation ignores photo-inhibition. Alternatively, one can use the two-parameter Platt et al. (1980) equation:

$$f_{lim}(E) = 1 - \left[1 - e^{\left(\frac{\alpha E}{P_{max}}\right)} \right] \left[e^{\left(\frac{-\beta E}{P_{max}}\right)} \right] \quad (2.12)$$

where β is the intensity at the onset of photo-inhibition. Figure 2.5 illustrates the light limitation functions or PE curves presented above.

2.2.4 Nutrient Limitation

Growing phytoplankton needs a steady supply of resources to maintain growth. Nutrient uptake and growth kinetics are usually described using Monod or Droop kinetics. The former is the simpler model and normally used for steady-state conditions, while the Droop or internal quota model is preferred for transient conditions, e.g. in fluctuating environments. The equation for nutrient limitation following Monod kinetics is:

$$\mu = \mu_{max} \frac{S}{(S + K_{\mu})} \text{ or } f_{lim}(S) = \frac{S}{(S + K_{\mu})}, \quad (2.13)$$

where S is the substrate concentration of the medium water, $f_{lim}(S)$ is the nutrient limitation function, μ_{max} is the maximal growth rate, and K_{μ} is the half saturation constant for growth.

The Droop equation expresses growth rate as a function of the cellular quota (Q) of the limiting nutrient (Droop 1970):

$$\mu = \mu'_{max} \frac{Q - Q_{min}}{Q} \quad (2.14)$$

where Q_{min} is the minimum cellular quota for growth. Maximum growth rate on substrate (μ_{max}) and cellular quota (μ'_{max}) are related via $\mu_{max} = \mu'_{max} \frac{Q_{max} - Q_{min}}{Q_{max}}$ where Q_{max} is the maximum cellular quota if S increases.

2.3 From Theory and Axenic Mono-Cultures to Mixed Communities in the Field

Progress in theory, creativity in experimental design, and dedicated hard laboratory work has generated process-based understanding of phytoplankton growth in the laboratory. This body of knowledge has deepened our understanding and guided our modelling efforts and field observation strategies, but we need to make many assumptions before we can apply this mechanistic approach to the field.

Let us return to our master Eq. (2.1): $P = \mu \cdot B \cdot f_{lim}$ (resources, environmental conditions). Ignoring environmental conditions, such as temperature, and substituting the simplest expressions introduced above we arrive at:

$$P = \mu_{max} \cdot B \cdot \frac{E}{(E + K_E)} \cdot \frac{S}{(S + K_\mu)} \quad (2.15)$$

This equation for primary production contains 6 terms that need to be quantified for the case of a single limiting nutrient and a single phytoplankton species. The light availability (E) and nutrient concentration (S) display spatial and temporal gradients in nature, and the maximum growth rate μ_{max} and half-saturation dependences (K_E and K_μ) require experimental or laboratory studies.

2.3.1 Does Diversity Matter or Not?

One of the most critical restrictions on the use of mechanistic complex models is related to phytoplankton diversity. Hutchinson (1961) identified the paradox that phytoplankton is highly diverse, despite the limited range of resources they compete for, in direct contrast to the competitive exclusion principle (Hardin 1960). Seawater typically contains tens of different species of primary producers, many for which there are no maximum growth data and known limitation functions. Accordingly, it is not feasible to simply apply Eq. 2.15 to individual species in the field and sum their contributions to obtain the primary production. Besides these theoretical arguments against the single species approach, there are also empirical reasons. Primary production and its dependence on environmental conditions (nutrients, temperature, light) are normally quantified at the community level in the absence of techniques to quantify species-specific primary production in natural waters. This discrepancy between, on the one hand, mechanistic, single-species approaches in the laboratory and, on the other hand, quantification of community responses and activities is somewhat unfortunate (Box 2.2).

2.3.2 Chl the Biomass Proxy

The biomass of the primary producer (B) is the second term in our master equation and quantifying this term in natural systems is more difficult than one initially would anticipate. Particulate organic carbon (POC) concentrations (g C per unit volume) are a direct measure of phytoplankton biomass in laboratory settings with axenic cultures. However, in natural systems, the pool of particulate organic carbon comprises not only a mixture of phytoplankton species, each with its own maximum growth rate, temperature, light and nutrient dependence, but also a variable and sometimes dominating contribution of detritus (dead organic matter), bacteria and other heterotrophic organisms. It is for this reason that *chl*orophyll concentrations (*Chl*) are used as a proxy for living primary producer biomass. The rationale is that *Chl* is only produced by photosynthesizing organisms, degrades readily after death of the primary producers and can be measured relatively easily using a number of methods. Primary producer biomass (B) can then be calculated if one knows the C:*Chl* (or *Chl*:C) ratio of the phytoplankton. However, this ratio differs among species and depends on growth conditions, in particular light and nutrient availability (Cloern et al. 1995). *Chl*:C ratios vary from ~ 0.003 to ~ 0.055 (gC g*Chl*⁻¹; Cloern et al. 1995), complicating going from phytoplankton growth to primary production. The very reason that *Chl* is such a good proxy for photosynthesizing organisms is also the reason why it is not well suited to the task of partitioning itself among different phytoplankton species: it is in all primary producers harvesting light energy. Accessory and minor pigments such as zeaxanthine and fucoxanthine, do, however, have some potential to resolve differences among phytoplankton groups, but not at the species level.

2.3.3 Light Distribution

The distribution and intensity of photosynthetically active radiation in seawater is governed by the intensity at the sea surface (E_0) and scattering and absorption of light, with the result that light attenuates with depth. The decline of light intensity E with water depth z can be described by a simple differential equation, expressing that a constant fraction of radiation is lost:

$$\frac{dE}{dz} = -k_{PAR}E \quad (2.16)$$

where the proportionally constant k_{PAR} is known as the extinction coefficient (m⁻¹). Solving this equation using the radiation at the seawater-air interface (E_0) yields the well-known Lambert–Beer equation:

$$E = E_0 e^{-k_{PAR}z} \quad (2.17)$$

The extinction coefficient k_{PAR} includes the absorption of radiation by water (k_w), by the pigments from various primary producers (k_{Chl}), by coloured dissolved organic matter (k_{DOC}), and by suspended particulate material (k_{spm}). The light extinction coefficient of pure water ($k_w \approx 0.015\text{--}0.035 \text{ m}^{-1}$) depends on the wavelength of light, with longer wavelength (red) being adsorbed more strongly than shorter wavelengths (blue); this is the cause of the blue appearance of clear water. The other light extinction components have a different wavelength dependence: the attenuation coefficients of dissolved organic matter (k_{DOC} ; “gelbstoffe”) and detritus (k_{SPM}) increase with shorter wave length, while that of phytoplankton (k_{Chl}) varies depending on the species, i.e. the pigment composition of the primary producers (Kirk 1992; Falkowski and Raven 1997).

Oceanographers often divide ocean waters into two classes with respect to light absorption: case 1 waters in which phytoplankton ($<0.2 \text{ mg Chl a m}^{-3}$) and its debris add only to k_w , and case 2 waters which have high pigment concentration and light attenuation because of (terrestrially derived) dissolved organic carbon and suspended particulate waters. The overall light attenuation (k_{PAR}) in case 1 waters can be approximated by (Morel 1988):

$$k_{PAR} = 0.121 \times Chl^{0.428} \quad (2.18)$$

where Chl is in mg Chl a m^{-3} .

Other useful empirical relations link light attenuation (k_{PAR}) to the Secchi depth (z_{Sec} , m), the depth at which a white disk disappears visually:

$$k_{PAR} = \frac{q}{z_{Sec}}, \quad (2.19)$$

where q varies from 1.7 in case 1 waters to 1.4 in case 2 waters (Gattuso et al. 2006) and

$$k_{PAR} = 0.4 + \frac{1.09}{z_{Sec}} \quad (2.20)$$

for turbid estuarine waters (Cole and Cloern 1987).

Light attenuation coefficients vary from 0.02 m^{-1} in oligotrophic waters, 0.5 m^{-1} in coastal waters, and to $>2 \text{ m}^{-1}$ in turbid waters. Light attenuation by water and phytoplankton dominate in the open ocean and on the shelf. In other coastal waters, including estuaries, phytoplankton and suspended particles dominate light attenuation, while light attenuation is primarily due to suspended particles in more turbid systems (Heip et al. 1995).

The light attenuation governs the euphotic zone depth (z_{eu} , m), i.e., the depth where radiation is 1% of the incoming:

$$\ln 0.01 = -k_{PAR}z_{EU} \text{ or } z_{EU} = \frac{4.6}{k_{PAR}} \quad (2.21)$$

Fig. 2.6 Conceptual figure of euphotic zone depth (solid black line) as a function of suspended particulate matter (SPM, mg L^{-1}) and phytoplankton concentrations (*Chl*, mg m^{-3}). The euphotic zone is more >200 m in the clearest ocean water with very low phytoplankton and light attenuation by water itself dominates. In most of the ocean, phytoplankton dominates light attenuation and euphotic zone depth scales with phytoplankton concentration. In estuaries and other turbid systems, dissolved organic matter and in particular suspended particles attenuate light and the euphotic zone narrows to less than one meter. Coastal systems and eutrophic parts of the ocean are in between. Case 1 and 2 oceanic waters are indicated. Light attenuation due to phytoplankton was modelled following Morel (1988; Eq. 2.18), while that due to suspended particles followed Cloern (1987) and euphotic depth was calculated as $4.6/k_{\text{PAR}}$

The euphotic zone is a key depth horizon in aquatic sciences because photosynthesis is largely limited to this zone. Moreover, the bottom of the euphotic zone is often used as reference for export of organic matter. Euphotic zone depths vary from about 200 m in the oligotrophic ocean, to tens of meters in shelf systems, to meters in coastal waters and a few decimetres in turbid and/or eutrophic estuaries (Fig. 2.6).

2.4 Factors Governing Primary Production

Having presented the factors governing phytoplankton production in laboratory studies and the limitations in applying that knowledge to natural systems, we have all the ingredients to explore the factors governing the (depth) distribution and rate of primary production in natural ecosystems.

2.4.1 Depth Distribution of Primary Production

Consider a system with a light profile following the Lambert–Beer equation (2.17) with $E_o = 10 \text{ mol m}^{-2} \text{ d}^{-1}$ and $k_{\text{PAR}} = 0.1 \text{ m}^{-1}$ (corresponding to a euphotic zone of 46 m) and a nutrient pattern as shown in Fig. 2.7. Nutrients are low in the upper 25 m ($N = 0.1 \text{ } \mu\text{mol m}^{-3}$) and then exponentially increase with a depth coefficient 0.1 m^{-1} to a maximum of $10 \text{ } \mu\text{mol m}^{-3}$.

If we further assume (1) that physical mixing homogenizes phytoplankton biomass ($B = \text{constant}$), (2) that there is only one limiting nutrients (N), and (3) that light and nutrient limitations can be described by Monod relations with parameter K_E and K_N . This allows combining μ_{max} and B into a depth independent maximal production P_m . The modelled P is then:

$$P = P_m \frac{E}{(E + K_E)} \cdot \frac{N}{(N + K_N)} \quad (2.22)$$

Taking K_N and K_E values of 1, i.e. 10% of E_o and maximum N at depth, and combining Eq. 2.22 with the light and nutrient profiles, we can then calculate the primary production as a function of depth (Fig. 2.7, green curve). Although these light and nutrient profiles and the model parameters K_N and K_E numbers have been chosen arbitrarily, they are reasonable and generate a representative depth profile for primary production with a subsurface maximum, as observed as a deep chlorophyll maximum (Fig. 2.8). In the upper 25 m, primary production is rather low because of nutrient limitation and declines slightly with depth because of light attenuation (Fig. 2.7). Primary production is optimal at depths between 25 and 40 m, i.e. where the nutricline and the lower part of the euphotic zone overlap. Primary production below 25 m is primarily light-limited, but accounts for about 75% of the depth-integrated primary production. Increasing surface-water nutrient concentrations or the phytoplankton affinity for nutrients (lowering K_N) would increase primary production in the top 25 m, but not so much at depth (Fig. 2.9a). Increasing the photosynthetic performance at low light levels (lowering K_E) would increase primary production at depth (Fig. 2.9b). Phytoplankton living in the surface ocean can thus optimize their performance by investing in nutrient acquisition, while those living in the subsurface would best optimize their light harvesting organs. This simple model explains why deep chlorophyll maxima occur in low-nutrient systems and why the depth distribution of primary production follows light in eutrophic systems (e.g. during early spring in Bermuda Atlantic station, Fig. 2.8).

2.4.2 Depth-Integrated Production

The overall control of light on depth-integrated production underlies satellite-derived algorithms for primary production and coastal predictive equations. For ecosystem and biogeochemical studies, the focus is on net primary production, i.e. carbon fixation minus phytoplankton respiration, expressed per m^2 and unit time

Fig. 2.7 Light and nutrient distribution versus depth and resulting primary production. The subsurface maximum often results in a deep chlorophyll maximum

Fig. 2.8 Fluorescence data at station BATS (Bermuda Atlantic Time Series) in February and August 1996

(day, year). Behrenfeld and Falkowski (1997) showed that depth-integrated net primary production (P , $\text{g C m}^{-2} \text{ yr}^{-1}$) can be estimated as:

$$P = P_{opt} \times Chl \times z_{eu} \times DL \times f_{lim}(E) \tag{2.23}$$

Fig. 2.9 **a** The impact of nutrient availability on the vertical distribution of primary production. Low half-saturation constants K_N imply high availability of nutrient for phytoplankton. **b** The impact of light harvesting efficiency on primary production. A high affinity (low K_E) for light causes higher primary production at depth. The nominal run is presented in Fig. 2.7

where P_{opt} is the maximum daily photosynthesis rate ($\text{mg C (mg Chl)}^{-1} \text{ h}^{-1}$), z_{eu} is the euphotic zone depth, DL is day length (h), and $f_{lim}(E)$ is a light limitation function. The similarity with our master Eq. (2.1) is evident, when nutrient limitation and environmental conditions are ignored. Integrating (Eq. 2.1) with depth to z_{EU} , and with time to sunset, we arrive at:

$$P = \int_0^{z_{EU}} \int_{sunrise}^{sunset} \mu_{max} \cdot B \cdot f_{lim}(E) \quad (2.24)$$

which is identical to (2.23), with $P_{opt} = \mu_{max}$; $Chl = B$, $\int_0^{z_{EU}} = z_{eu}$, and $\int_{sunrise}^{sunset} = DL$.

Behrenfeld and Falkowski (1997) showed that 85% of the variance in global net primary production can be attributed to depth integrated biomass ($Chl \times z_{eu}$) and the maximal photosynthesis parameter P_{opt} , with other factors, such as differences in light limitation functions, depth distributions of phytoplankton biomass and day length (DL), being less important. Consequently, the most rudimentary model would be (Falkowski 1981):

$$P = \psi \times Chl \times z_{EU} \times E_o \quad (2.25)$$

stating that net primary production (P) scales linearly with depth integrated biomass ($Chl \times z_{EU}$), incoming radiation (E_o) and an optimal photosynthetic parameter (ψ). Similar semi-empirical relations are often used in estuaries (Cole and Cloern 1987; Heip et al. 1995):

$$P = a + b(Chl \times z_{EU} \times E_o) \quad (2.26)$$

where a and b are regression coefficients that are system specific.

2.4.3 Critical Depths

The overall governing role of light on primary production and phytoplankton dynamics also underlies the use of two critical depth horizons, often credited to Sverdrup (1953): the compensation depth (z_c) and critical depth (z_{cr}). These were introduced to understand and predict spring blooms in the ocean. At the compensation depth (z_c), phytoplankton photosynthesis is balanced by community respiration (Fig. 2.10), i.e. the depth of the radiation level at which photosynthesis (by phytoplankton) compensates their respiration (E_c). This compensation depth should not be confused with the physics governed mixed-layer depth (z_{mld}) and the critical depth (z_{cr}), where primary production integrated through the water column and over the day will equal the daily water column integrated community losses of carbon (Sverdrup 1953; Fig. 2.10). These depths are pivotal to the formation of

Fig. 2.10 Production and respiration (left) and depth integrated production and respiration (right) as a function of water depth. The critical depth is where depth integrated production and respiration balance (200 m), the compensation depth is where production and respiration of phytoplankton balance (30 m). The euphotic zone is governed only by light attenuation and is 46 m. P_0 is $30 \text{ mol m}^{-2} \text{ d}^{-1}$; R_0 is $0.05 \cdot P_0$; $E_0 = 30 \text{ mol m}^{-2} \text{ d}^{-1}$; $k_{PAR} = 0.1 \text{ m}^{-1}$

phytoplankton blooms in the oceans (Sverdrup 1953). If the mixed layer is deeper than the critical depth (z_{cr}), then phytoplankton will spend relatively too much time at low irradiances and carbon losses are not compensated by sufficient growth. Conversely, if the mixed layer is shallower than z_{cr} , phytoplankton communities can grow and blooms can develop. Assuming that carbon losses (R_o) are constant with depth, there is no nutrient limitation, and gross primary production is linearly related to radiation, which in turn depends exponentially on depth (Eq. 2.18), primary production is described by:

$P = P_0 e^{-k_{PAR}z}$, where P_0 is the surface productivity. One eventually arrives at following relations for Sverdrup's critical depth, z_{cr} :

$$\frac{(1 - e^{k_{PAR}z_{cr}})}{k_{PAR}z_{cr}} = \frac{E_C}{E_0} = \frac{R_0}{P_0} \quad (2.27)$$

where E_c is the radiation level at the compensation depth and R_o is the depth-independent community respiration rate (Sverdrup 1953; Siegel et al. 2002). Clearly, light attenuation is a major factor, not only governing z_{eu} , but also z_c and z_{cr} . The critical depth (z_{cr}) is usually 4 to 7 times higher than the euphotic zone depth (z_{eu}). The compensation depth (z_c) is typically 50–75% of the euphotic zone depth (Siegel et al. 2002; Sarmiento and Gruber 2006; Fig. 2.10). For simplicity, the compensation depth is often taken equal to the euphotic zone depth; this should be discouraged, because it implies that community respiration represents only 1% of maximal production. The depth of the euphotic zone (z_{EU}) is an optical depth governed by the light attenuation and thus only indirectly impacted by phytoplankton via their effect on k_{PAR} , while the compensation depth depends on the community structure (algal physiology and heterotrophic community). The Sverdrup critical depth model is simple, instructive and predictive: it can explain bloom initiation when mixed layers shallow and link it to physical sensible and quantifiable parameters. However, it is sometimes difficult to apply because of inconsistencies and uncertainties in the parameterisation (phytoplankton vs. community respiration and other phytoplankton losses) and the validity of the assumptions (no nutrient limitation, well-mixed layer).

The critical depth horizon concept has been developed for deep waters, but a similar approach can be applied to shallow ecosystems. In shallow coastal systems, it is the relative importance of water depth and euphotic zone depth that governs (a) where production occurs and (b) whether phytoplankton biomass will increase or not. If water depth is less than the euphotic depth (z_{EU}) light reaches the seafloor and primary production by microbial photoautotrophs (microphytobenthos), as well as macroalgae and seagrasses, may occur. Gattuso et al. (2006) showed that this may happen over about 1/3 of the global coastal ocean. If water depth exceeds the euphotic zone by more than a factor 4–7 then phytoplankton losses in the dark cannot be compensated fully by photosynthesis and phytoplankton communities will lose biomass (Cloern 1987; Heip et al. 1995). Vice versa, if water depth <4–7 times Z_{EU} phytoplankton growth is maintained. Consequently, shallowing of ecosystems (e.g. water flowing over a tidal flat or development of stratification)

Fig. 2.11 Conceptual picture of phytoplankton bloom in estuarine plume

stimulates phytoplankton community growth, all other factors remaining equal, while deepening of water bodies will cause a decline. Moreover, in turbid systems where the light attenuation (k_{PAR}), and thus z_{EU} (Fig. 2.7), are governed by suspended particulate matter dynamics, phytoplankton communities may experience variable twilight conditions and have difficulty maintaining positive growth. Consequently, when turbid rivers and estuarine waters with high nutrients reach the sea, particles settle and light climate improves, phytoplankton blooms may develop and utilize the nutrients (Fig. 2.11).

Sverdrup's critical depth hypothesis is based on the assumption that phytoplankton biomass and phytoplankton losses are homogeneously distributed in the mixed layer. However, the mixed layer with uniform temperature as used in Sverdrup's approach does not match with the layer of turbulent mixing in the ocean (Franks 2015). It is more realistic to represent phytoplankton biomass (B) as governed by the balance between production, respiration losses and transport by eddy diffusion and particle settling. Again, we assume gross primary production is linearly related to radiation (which declines exponentially); hence: $P = P_0 e^{-k_{PAR}z}$. Phytoplankton respiration loss is considered a first order process: $Loss = rB$ with a first-order rate constant (r). Under the assumption of steady-state we then arrive at (see Box 1.1):

$$K_z \frac{d^2 B}{dz^2} - w \frac{dB}{dz} - rB = P_0 e^{-k_{PAR}z} \quad (2.28)$$

where K_z is the vertical eddy diffusion coefficient (m^2s^{-1}), w is the settling velocity (m s^{-1} ; positive downwards), the other terms have been defined before. Considering a semi-infinite domain, i.e. $\frac{dB}{dz} = 0$ at large depth, and phytoplankton biomass B_0 at the water-air interface, we obtain the following solution:

$$B = \left(B_0 - \frac{P_0}{K_z k_{PAR}^2 + w k_{PAR} - r} \right) e^{\alpha z} + \frac{P_0}{K_z k_{PAR}^2 + w k_{PAR} - r} e^{-k_{PAR} z} \quad (2.29)$$

with $\alpha = \frac{w - \sqrt{w^2 + 4rK_z}}{2K_z}$.

The second exponential term accounts for light-dependent production, while the first exponential comprises water-column mixing, phytoplankton settling, and phytoplankton losses. To simplify matters, we assume that phytoplankton biomass is zero at the air-water interface. The first and second term then balance if $\frac{w - \sqrt{w^2 + 4rK_z}}{2K_z} = -k_{PAR}$. After re-arrangement to isolate the eddy diffusion coefficient, we obtain

$$K_z = \frac{r - k_{PAR} w}{k_{PAR}^2} \quad (2.30)$$

In other words, the vertical eddy diffusion coefficient K_z should be less than $\frac{r - k_{PAR} w}{k_{PAR}^2}$ for positive values of phytoplankton biomass (B).

Huisman et al. (1999) presented a more elaborate model on phytoplankton growth in a turbulent environment, including a feedback between phytoplankton biomass and k_{PAR} . Through scaling and numerical analysis of a model without phytoplankton sinking ($w = 0$), they derived a relationship between the maximum turbulent mixing coefficient K_z and k_{PAR} : $K_z = \frac{0.31}{k_{PAR}^2}$. If we also ignore phytoplankton advection ($w = 0$ in Eq. 2.30), $K_z < \frac{r}{k_{PAR}^2}$, fully consistent with Huisman et al. (1999). The critical turbulence level for phytoplankton growth is thus inversely related to the square of the attenuation of light. Moreover, the phytoplankton loss is the scaling factor. For turbid systems such as estuaries and other coastal systems with high light attenuation (k_{PAR}), turbulent mixing should be minimal to allow net growth, consistent with observations by Cloern (1991) that phytoplankton blooms develop during neap tide when turbulent mixing intensity is lowest. Conversely, in clear, oligotrophic waters, light attenuation is limited and phytoplankton blooms can occur at relatively high mixing rates. Sinking phytoplankton ($w > 0$) will lower the numerator of Eq. 2.30 and thus lower the critical turbulence levels, while buoyant phytoplankton ($w < 0$) will increase the maximal allowable turbulence, and thus the scope for phytoplankton growth.

Fig. 2.12 Production as a function of individual biomass for a wide variety of organisms, including animals, plants and prokaryotes (based on data compiled by Hatton et al. (2015))

Box 2.1: Phytoplankton size based traits

The intrinsic maximum growth of phytoplankton varies with size (Fig. 2.2). Metabolic activity of organisms usually scales with size and when expressed in terms of mass or volume (V) follows a simple power law

$$\mu = aV^b, \tag{2.31}$$

where $b = -0.25$ according to the metabolic theory of ecology (Brown et al. 2004). Accordingly, the smaller the organism, the higher the intrinsic maximum growth rate. This power law relationship holds over orders of magnitude and across a wide range of organisms (autotroph and heterotroph,

eukaryotes and prokaryotes; e.g., Fenchel 1973) and implies that smaller organisms have the highest intrinsic growth (Fig. 2.12).

However, some cell components are non-scaleable, such as the genome and membrane, and consequently this power-law appears to break down in the range of nanoplankton (2–20 μm). There is a trade-off between the size dependence of physiological traits (Ward et al. 2017). Burmaster's (1979) equation can be used to illustrate this:

$$\mu_{\text{size}} = \frac{\mu_{\text{max}} \cdot \theta_{\text{size}}}{\mu_{\text{max}} \cdot Q_{\text{min}} + \theta_{\text{size}}}, \quad (2.32)$$

where the maximum growth for a certain size (μ_{size}) depends on maximum nutrient uptake (θ_{size}), minimum cell quota (Q_{min}) and theoretical maximum growth rate (μ_{max}). Maximum nutrient uptake and requirement per cell scale positively with cell size (Fig. 2.2b, dashed blue line), while theoretical maximum growth rates scale negatively (Fig. 2.2b solid blue line). The result is an optimum in growth rate for phytoplankton in the nanoplankton range (Fig. 2.2b, black line). Very small picoplankton cells have a low intrinsic growth rate that will increase with size because more volume is then available for catalysing and synthesizing. The intrinsic growth rate of microplankton cells will decrease with increasing size, as with most organisms, for multiple reasons, including the increase in intracellular transport distances between cellular machineries (Marañón et al. 2013).

Box 2.2: Phytoplankton diversity, rate measurements and biogeochemical models

The high number of different species in each water sample poses a challenge to link the species-specific growth parameters obtained in the laboratory with measurements of phytoplankton growth in the field and modelling of phytoplankton primary production for natural, mixed communities. Gross primary production is normally quantified by the production of oxygen, using either ^{18}O -labelling or the differential evolution of oxygen in light and dark. The most common technique for measuring primary production is the ^{14}C labelling technique, but this method provides a result in between gross and net photosynthesis, depending on the duration of the incubation. Both approaches quantify primary production for the total community, rather than for specific species. Biological oceanographers have developed methods to quantify group-specific primary production, based on dilution approaches or the incorporation of isotopically labelled bicarbonate into biomarker or flow-cytometry separated groups of organisms (Laws 2013). These group-specific primary production measurements can be compared more directly to laboratory data.

Biogeochemical modellers have explored a number of strategies to incorporate differences among phytoplankton species into their ecosystem models; e.g. the plankton functional group approach and phytoplankton size or trait based approaches. The former approach is limited to a few plankton groups that are representative for certain biogeochemical fluxes (e.g. N_2 -fixers, diatoms, small and large phytoplankton, coccoliths; Sarmiento and Gruber 2006). The size-based approach makes use of the systematic relationships between phytoplankton size and activity (e.g. Fig. 2.2), but some processes do not scale in a simple way with size. Trait- and genome-based approaches are the most recent, and they consider emergent phenomena (Follows et al. 2007). These approaches are instructive and needed to further our understanding and predictive capabilities in times of global change, but they are so far difficult to link with observations in the field.

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