

On the definition of plankton production terms

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The development of our plankton production terminology is discussed. It has been necessary to take into consideration, successively, algal and community respiration, as loss terms; when community processes are dealt with, space, time, and the size and abundance of the individual organisms also become considerations. No agreement exists as to whether the primary processes themselves (i.e., photosynthesis and respiration) should be defined in terms of energy or material flux. An argument is presented to illustrate that our methodology is now more precise than our definitions, and a start is made to formulate a consistent set of definitions.

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Introduction

It must be axiomatic that one cannot measure what is not defined, and that the accuracy of our measurements is no better than that of our definitions. A number of authors have discussed the terminology of ecosystem productivity. A prevailing view is that the definitions are wanting; the extreme view is apparently taken by Ohle (1956), who is cited by Davis (1963) to conclude that the term productivity has been defined by so many authors in so many ways that it might be best if it were eliminated entirely from our scientific vocabulary. Flynn (1988) argues that another commonly used term – primary production – is likewise sufficiently imprecise that it should either be defined properly or discarded. However, if my axiom is accepted and if we are unable to define ecosystem production terms with any precision then we must accept that we are unable to interpret our ecosystem measurements, which would call into question the value of making the measurements in the first case. The last two decades have seen the evolution of a variety of methods to measure planktonic production. Certainly it is my impression, as I shall attempt to argue further on, that we are in the position that our methods are more precise than our definitions; which is surely an unsatisfactory state of affairs.

In this essay I consider at some length the existing definitions of the various planktonic production terms; in doing so I attempt to bring out the development of concepts associated with the various terms. Some of this ground has been gone over before, key papers being those of Macfadyn (1948) and Davis (1963), and accord-

ing to Macfadyn the paper of Thienemann (1931). I have attempted to assimilate their arguments into the present text.

I conclude by offering a set of definitions which are intended to be consistent and useful and which will give us a basis with which to examine the accuracy of our production methods. The evolution of concepts and terminology is summarized in Fig. 1.

The beginnings

The notion of ecosystem productivity certainly dates back to the nineteenth-century chemist Liebig and no doubt beyond. There is little gained from considering the early history in the present account; this has been done by Macfadyn (1948). A convenient starting point for the present account is the paper of one of the pioneers of the study of aquatic production: Gordon Riley. In 1940 he provided a comprehensive set of definitions; significantly he distinguished between what we would call gross production and loosely call net production:

The biological productivity of a lake must strictly be defined as the rate of production of organic material in the lake.... In defining phytoplankton productivity it is necessary to make a distinction between the mere synthesis of organic substance, fundamentally glucose, and the elaboration of new organisms from the products of photosynthesis, ...

He then goes on to define his terms:

Gross productivity: The rate of production of organic matter by the photosynthetic activity of the phytoplankton.

Phytoplankton productivity: The rate of production of phytoplankton organisms. These either increase or replace the organisms of the standing crop.

And makes the point:

The above definitions are in accord with limnological theory, for they permit the application of standard mathematical procedures to the dynamic aspects of ecological relationships. Technical difficulties, however, prevent their immediate application to practical limnological problems. The closest approach that can be made at present is an estimate of the mean rate of production during a specified unit of time.

He continues:

But since there appears to be no practical advantage to be gained in dealing with mean rates, the following empirical definitions are proposed:

Gross production: The amount of photosynthetic activity occurring during a given unit of time, expressed as units of glucose, oxygen, energy, or any other term in the equation for photosynthesis.

Phytoplankton production: The quantity of phytoplankton produced during a given unit of time, expressed as the weight of dry organic matter.

Loss at the primary autotroph level and the concept of net production

In defining his term "plankton productivity" Riley was acknowledging the loss terms inherent in the concept of net production. Respiration had been long recognized as a loss term and this was clearly in the mind of the authors of a report prepared by Cushing. He chaired a group of experts (Cushing *et al.*, 1958) brought together under the auspices of the ICES. They first defined the basis of measurement:

Primary productivity: the carbon "fixed" per m^2 or per m^3 /unit time.

The use of carbon clearly reflects the pre-eminence of the ^{14}C technique for making production measurement of marine plankton at that point in time. The committee felt it important to note that the measurements should be taken right through the photic zone. There was no definition of what was meant by the term photic zone, which because of the logarithmic decrease of light with depth was not critical in the case of the calculation of areal gross production but is crucial when respiration enters into consideration, i.e., in the calculation of net

production. They then went on to define gross and net production:

Gross primary production: the quantity of carbon taken up into organic combination.

To obtain the net primary production, a correction must be made for respiration; to make this correction, the gross primary production should be calculated from sunrise to sunset and the loss by respiration, calculated for a 24 hour period.

It should be noted that the organisms responsible for the respiration were not defined; to be consistent with other definitions one must presume they were thinking of algal respiration.

In passing, they note: "Each of the terms given above can also be expressed as energy." Thus effectively we are left with two definitions of production, one based on *energy*, one based on *material* (carbon). Here we have a very significant division, to which I shall return in the section entitled "The basis of measurement of photosynthetic and respiration rates".

In 1960, a thoughtful and comprehensive set of definitions was produced by the chemist John Strickland. The precision of these definitions reflects Strickland's rigorous background as an analyst and his approach to aquatic ecology. Still thirty years later they are the set one refers back to for guidance.

He starts by defining net and gross production:

Net primary production: The net rate of autotynthesis of the organic constituents of plant material in water. This will again be measured on the basis of organic carbon per unit volume or beneath unit area of sea surface, with the time scale chosen to suit a particular context. The definition is limited to the primary productivity of plant material and, by virtue of the methods used, generally refers to productivity from inorganic sources of carbon. The measurement does *not* include the rate of loss of primary material by death or predation.

Gross primary production: The definition and units are the same as those used above for net productivity except that the rate under consideration is the gross rate of the photosynthetic increase in plant crop before any corrections for respiration or excretion are made.

Note that Strickland in his definition of net primary production made it clear that the respiration was algal, thus tightening up Cushing *et al.*'s (1958) definition.

The last sentence of the above definition I have found to be somewhat ambiguous, which I am sure was not Strickland's intention. I read it to mean that included in net primary production is any material lost, over the period considered, to grazing, death, and also (very importantly) one would expect it to include organic excretion losses. This interpretation is consistent with the statement elsewhere in his text.

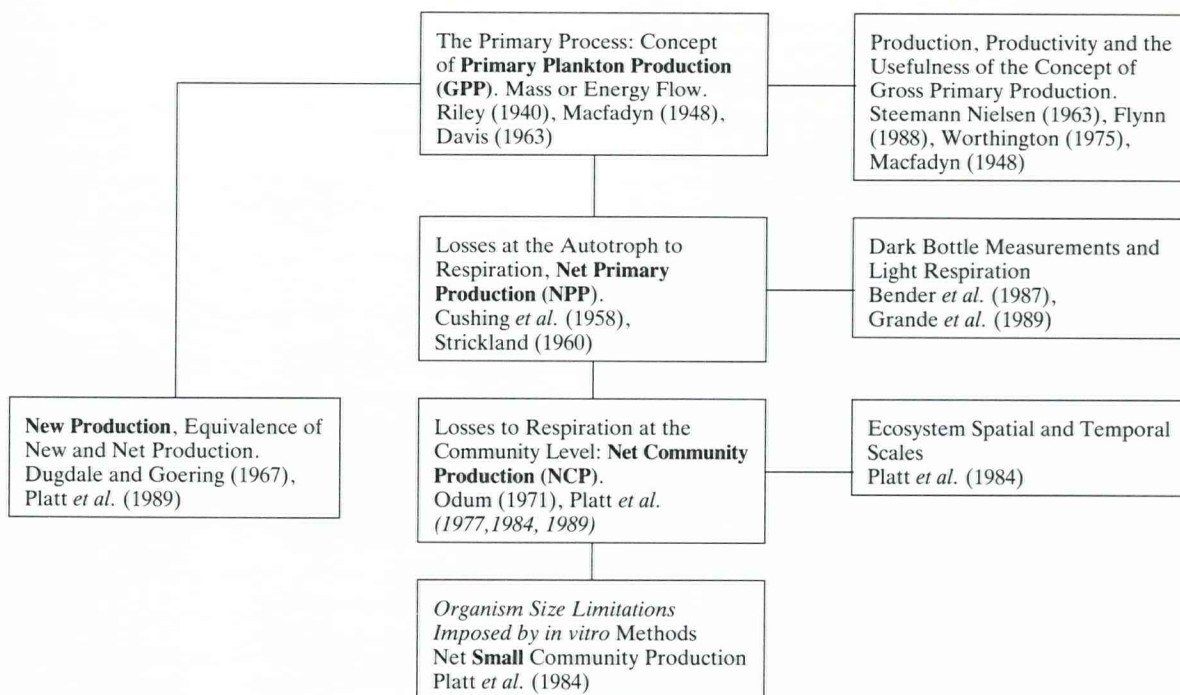


Figure 1. Evolution of terminology.

The terms gross and net are used in conjunction with photosynthesis to distinguish between the true synthesis of organic matter resulting from exposure to light (gross) and the net formation of organic matter that is found after allowance has been made for the respiration and other losses that occur simultaneously with the photosynthetic processes.

Strickland also defines net production rate:

Net production rate: this term should be reserved to describe the rate of production (either positive or negative) of plant organisms under the influence of all environmental factors and thus include losses by death and predation.

This defines a term distinct from net primary production and in doing so clarifies his definition of net primary production. As defined, net production rate would not take into account simultaneous losses at other trophic levels, e.g., bacterial respiration of excreted organic material. The term essentially refers to net autotroph accumulation. It is important to note that this term is not equivalent to net community production as might be measured by, for example, the oxygen technique. Strickland, in defining his term, makes no specific reference to losses by release of exudates; this omission we should not see as intentional; at the time Strickland produced his definitions this form of loss was not widely

considered by aquatic ecologists. We may expect that Strickland would have considered this as a loss term. In doing so, it would make the term equivalent to net particulate production (P_p) as defined by Platt *et al.* (1977).

The next set of definitions comes from the review article by Steemann Nielsen (1963).

Gross primary production: rate of real photosynthesis

Net primary production: rate of real photosynthesis less the rate of respiration by the algae.

These definitions are quite clear except that they presume we have a definition of or understand what is meant by "real photosynthesis". One may suspect that Steemann Nielsen, by "real", was thinking of the primary photosynthetic process, but it would have been useful had he made this clear.

Following this we have definitions by Odum (1971) of the terms gross primary productivity and net primary productivity. He also, see below, defines net community productivity.

Net primary productivity is the rate of storage of organic matter in plant tissues in excess of the respiratory utilization by the plants during the period of measurement. This is also called "apparent photosynthesis" or "net assimilation".

lation". In practice the amount of respiration is usually added to measurements of "apparent" photosynthesis as a correction in order to obtain estimates of gross production.

The qualification "storage of organic matter in plant tissues" would present little problem in terrestrial ecology but would for plankton make the term equivalent to Strickland's net production. In all probability, for aquatic microplankton the phrase "rate of storage ... tissues" would probably be replaced by "rate of photosynthetic formation of organic material", making the term equivalent to Strickland's definition of net primary production.

We now have two rates defined which take into consideration losses at the primary autotroph level. The first considers only losses due to respiration, the second includes all loss terms by the primary producers. The former is generally referred to as *net primary production* and the latter as *net production*. Net primary production is an important concept for modelling although in practice it is not clear if we are able to measure it. Net production is probably a less exact term but in principle easier to measure.

Extension to net community production and recognition of size, space, and time

Logically the next step is to consider the production of the community as a whole and this has resulted in a number of definitions, in part because when the measurements are made size, space, and time have to be taken into consideration. Odum (1971) defined the term taking a year as his time frame.

Net community productivity is the rate of storage of organic matter not used by heterotrophs (that is, net primary production minus heterotrophic consumption) during the period under consideration, usually the growing season or a year.

Odum avoids use of the ambiguous term net production. He goes on to make the very interesting recommendation:

The total energy flow at heterotrophic levels which is analogous to gross production of autotrophs should be designated as "assimilation" and not "production".

One sees the value of this in the case of so-called bacterial "production", which is sometimes treated as if it were primary production; the use of "assimilation" in place of production might serve as a check to avoid confusion.

Platt and his co-workers in a series of papers (Platt *et al.*, 1977, 1984, 1989) grapple with a variety of problems associated with the definition of production terms. They

(i.e., Platt *et al.*, 1977) very clearly state the perspective of their work:

Since we are more interested here in the ecological rather than the biophysical aspects of photosynthesis, and since our models have a strong empirical flavor, we adopt the carbon definition, which corresponds better with the measurement techniques used in oceanography.

They define the term:

Net productivity: Net productivity (P_n) is simply $P_g - R$.

Whereas the definition does not prescribe the source of the respiration, from the text I infer that it is algal. If so, Platt *et al.*'s net production term is not equivalent to Strickland's, which includes losses such as grazing in addition to respiration. As far as I can see, the term is equivalent to net primary production, as defined by Steemann Nielsen and Odum.

Platt *et al.* (1977) further define a useful ecological term net particulate production:

It is useful to distinguish also net particulate production (P_p) which differs from P_n by the rate of excretion (E) of organic carbon from the cell: $P_p = P_n - E$. For herbivores, P_p is the quantity of interest rather than P_n (although E of course may reappear in particulate form if assimilated by bacteria or adsorbed to inanimate particles).

They argue the value of this term in models:

We can conclude that models in which P_p is the dependent variable are to be preferred.

However, they follow this with the caveat:

It has to be admitted, however, that most of the models which treat "primary production" of phytoplankton purport to be models of P_g . Thus in what follows we use the unqualified term "primary production" and the unsubscripted symbol P ($\text{mgC}/\text{m}^3/\text{hr}$) to denote the dependent variable with the understanding that although the intent is usually to model P_g , other kinds of data have often been used for fitting and verification.

In a subsequent paper (Platt *et al.*, 1984) appear to further define particulate production; in doing so they draw attention to the size constraints of our *in vitro* field measurements:

Net small particulate production (P_n) is sometimes thought of as the net autotrophic productivity, but it also includes the transformations of organic matter (assimilation, respiration and excretion) by microheterotrophs.

They elaborate:

Operationally, P_n is equivalent to the light bottle O_2 changes during 24 h. We have elected to place 24 h ^{14}C productivity estimates in this category, but we recognize

that the interpretation of ^{14}C uptake rates is subject to discussion (Peterson, 1980).

I have found this definition confusing because it does not seem consistent with their earlier definition of P_n . I can only conclude that the terms are not intended to be equivalent and the use of the same notation is accidental. Certainly, in a subsequent paper (Platt *et al.*, 1989) the term P_n is clearly defined as net primary production equivalent to $P_g - R$, where R is made clear to be autotroph respiration (i.e., P_n is the same as in their 1977 paper, except that it is there called net productivity). Given that this is the case and that the term in the 1984 paper is purely an operational one, the process measured seems to be between equivalent to net community production (Odum, 1971) without the loss term due to meso-zooplankton grazing.

Platt *et al.* then go on to give a definition of net community production; in doing so they add a space constraint:

Net community production (P_c) is the rate of accumulation of organic matter within the euphotic zone plus the rate of export of organic matter from the euphotic zone.

They have chosen to include the export terms in their definition, which of course is necessary as it is intended to be an operational one.

New and net production

Dugdale and Goering (1967) introduced the term "new production" into the study of phytoplankton nitrogen dynamics to refer to primary production not supported by recycled nitrogen. The term is now widely used and it clearly has affinities with net production although the relationship is not straightforward. Platt *et al.* (1984, 1989) equate net community production (P_c) with "new production".

It (i.e., net community production) is "new production" in the sense of Dugdale and Goering (1967). As such, P_c is the excess of gross productivity (P_g) over community respiration. Direct observations of P_c include the accumulation rate of oxygen within the euphotic zone over an extended period (time scale of months), or the flux of sinking organic matter as measured by sediment traps or calculated from the respiration rates in the aphotic zone. In nutrient limited ocean provinces, P_c is constrained by the nitrogen flux to the euphotic zone, as discussed below.

At first sight there seem to be two apparent inconsistencies in equating new and net community production. The first is that whereas algal respiration in common with heterotroph respiration, results in the flux of carbon and oxygen, the former contrasts with the latter in that it does not result in production of inorganic nitro-

gen, thus algal respiration is included in net community production but not in new production, i.e. Net community production = $P_g - (R_a + R_h)$, whereas New production = $P_g - R_h$, where P_g = gross production, R_a = algal respiration, R_h = herbivore (microbial and meta-zoan) respiration, thus net community production $\leq$ new production.

This issue is picked up in a later paper by Platt's group (Platt *et al.*, 1989); they offer a neat resolution to the problem. On the assumption that the ^{14}C technique measures net primary production and that this technique is used to determine the rates of plankton photosynthesis (see their operational definition of P_n above), then the measurement will already be corrected for algal respiration, so in practice P_g (they use the term P_T) will, in fact, be $P_g - R_a$. Thus $P_T = P_g - R_a = P_r + P_{\text{new}}$, where P_r = regenerated production and P_{new} = new production.

Regenerated production (i.e., ammonia-based production) is based on heterotroph respiration. Thus $P_r = R_h$, therefore $P_T = P_g - R_a = R_h + P_{\text{new}}$, thus $P_{\text{new}} = P_g - (R_a + R_h)$, therefore $P_{\text{new}} = \text{Net community production}$.

At first it may seem something of a sleight of hand, but given the assumption that measured production is $P_g - R_a$, the argument appears to be sound.

It seems to me that there may be a problem at a second level equating new with net production, at least operationally and this needs airing. New production is a cumulative property of the community, whereas both net primary production and net community production can wax and wane. In a closed system P_c would be essentially zero on an annual basis. The answer to the inconsistency probably lies in working in appropriate temporal and spatial scales. It seems clear that if one considers a closed system, the equivalence between new production and net community production cannot be made. If one considers simply the process occurring in the euphotic zone, it should be possible to make the equivalence for the export process remove the constraint that P_c , on an annual basis, must be zero. In that case, assuming Redfield-type links between carbon and nitrogen, the export of carbon (i.e., the net community production of the euphotic zone) must be linked with the import of nitrate (i.e., new production) of the water column. On different (i.e., shorter) time scales and (greater) space scales the equivalence cannot be achieved or so it seems to me.

The basis of measurement of photosynthetic and respiration rates

So far in the present account the terms photosynthesis and respiration have been used but only passing refer-

ence has been made to what these processes entail and how they can be measured. When considered in detail there are wide departures between various authors.

In his 1960 paper Strickland attempts a definition of photosynthesis:

The rate of photosynthesis can be defined in at least three ways, according to the method of measurement used.

(i) The rate of increase of dry organic matter in plants that results from photosynthetic activity. This definition is rarely employed in work with algae and it is not often practicable to measure such a weight increase or to decide what fraction of the weight increase arises from photosynthesis and how much from heterotrophic growth.

(ii) The rate of increase of the amount of oxygen in the extracellular environment of plants that results from photosynthetic activity. This rate of increase is not necessarily the same rate as measured in (i) above, even on a molecular basis, as the plant material may not liberate all photosynthetically formed oxygen immediately and some uptake of carbon dioxide may occur without simultaneous oxygen liberation. However, for periods exceeding a few minutes, a pseudoequilibrium stage will probably be reached and the two measurements will be proportional to each other and related, in principle, by a suitable empirical factor.

(iii) The rate of decrease of the amount of carbon dioxide from the extra-cellular environment of plants that results from photosynthetic activity. This rate of decrease is not necessarily the same rate as in (i) or (ii) above, as the carbon dioxide taken in by a photosynthesizing system may not all be used at once or may only produce organic compounds of transient stability. However, for periods exceeding a few minutes, provided that a "dark uptake" blank is deducted, the measurements will be proportional and related by some factor.

Clearly Strickland, as a field scientist, was attempting useful and practical definitions of these terms whilst trying to retain rigour. Krebs (1972) in his book provides us with a definition of photosynthesis: "Photosynthesis is the process of transforming solar energy into chemical energy."

The important thing to note with the definitions is that it is based on energy transformations, rather than the production and consumption of organic material. Fogg (1980) takes a similar view of the process of primary production and provides a very valuable definition:

... primary production is defined as input of potential chemical energy into the ecosystem; all these processes – photoassimilation, bacterial photosynthesis, chemosynthesis and conversions of inorganic substances – ought to be taken into account.

The last point, the inclusion of the conversion of inorganic substance (e.g., the reduction of nitrate to ammonia) is a critical consideration when one attempts a rigorous definition of plankton production, as we shall see later.

In Platt *et al.* (1977), a number of definitions are given:

Gross primary productivity: It is possible to define gross

primary productivity (P_g) in a number of different ways. For example, P_g may refer to the rate at which radiant energy is used in the production of ATP and reduced NADP or it may refer to the rate at which inorganic carbon is incorporated into organic carbon in the cell. Note that these two definitions are not necessarily exactly equivalent. For example, some of the ATP formed in photophosphorylation may be exchanged across the chloroplast and would be unavailable as reducing energy in the dark fixation of CO_2 .

In a subsequent paper (Platt *et al.*, 1984) they adopt a very specific definition of gross production.

Gross primary production (P_g) is equal to the rate of photosynthetic conversion of light energy into chemical bond energy.

They used this to set the upper limit to water column production and then suggest how it can be measured.

Observations approximating P_g include short term (time scale ~ 1 hour) carbon fixation rates; 24 h light and dark bottle oxygen changes; and diel changes in dissolved oxygen, particulate organic carbon or dissolved inorganic carbon.

It should be noted that although the process is defined in energy units, the suggested measurements give rates in mass units. I am puzzled by the reference to diel studies as a means of obtaining gross primary production. Diel changes provide a measurement of net changes, i.e., net community production, although of course, given assumptions about the corrections for respiration gross production may, of course, be calculated.

It is very clear that there is no consensus over what constitutes a measurement of planktonic photosynthesis. The definitions fall into two classes. One set, which originates from algal physiologists, biochemists and fundamental ecologists (e.g. Steemann Nielsen, Krebs and Fogg) regard production as the biochemical injection of energy into the biosphere. The second set comes from community ecologists, modellers, biogeochemists (e.g. Riley, Strickland, Platt) who are concerned with the organism side of production, i.e., yields of groups within the food web, models of food webs. The former group base their definitions primarily on energy flow, the second on material flow and the argument given (in the section entitled "How good are our definitions compared with our methods of measurement") below illustrates that this difference in perspective can give rise to significant differences in what is and is not a correct measurement of planktonic production, and, as such, ultimately is a limit of the accuracy of our measurement of production.

In a very thoughtful article, Macfadyen (1948) discusses the problems of defining and measuring ecosystem productivity. He argues that the cycles of energy

and material are fundamentally distinct and of a different nature:

Whereas energy passes only once through an ecosystem and is utilised only by one animal on one occasion, matter is continuously circulating or in store; it does not leave the system (by definition).

He views matter as a vehicle for the flow of energy and is of the view that the casual exchange of energy and matter as measures of ecosystem productivity has led to confusion. He argues that the energy flux is conceptually tidier and makes the case for this as a basis for production; he prefers the term ecosystem activity measurement. We need to return to the argument later (in "Towards a consistent set of definitions").

Production or productivity

Various authors (e.g., Macfadyn, 1948; Davis, 1963; Steemann Nielsen, 1965; Flynn, 1988) have discussed the terms "production" and "productivity" and have come to the conclusion that owing to casual confused use or misuse, one or other of the terms should be abandoned. Macfadyn (1948) argues for starting again with the term "activity". The dictionary definitions (e.g., Little *et al.*, 1983) make it clear that whereas production (like product) is a concrete term, productivity is qualitative and more abstract. In discussing ecosystems, in addition to defined and measurable properties it is useful to have non-defined qualitative terms that allow one to refer to the very general properties of an environment, provided it is clear what is defined quantitatively and what is not. Production (or the rate of production) would seem to be the term to retain as the defined property ("... the annual production was ..."), whereas productivity (as fertility) is best retained for the qualitative description of the level of production ("... a period of high productivity ...").

Is gross production a useful ecological concept

In an important publication "The Evolution of IBP", Worthington (1975) struggles with the concept of gross production, its measurement and, more importantly, the usefulness of the term. He starts by attempting to define production rate:

Production rate is thus more rigorously defined as the rate of change of biomass plus the rate at which biomass, as individuals or parts of individuals, has been removed by death and subsequent microbial or other dissolution, by grazing, predation, cropping or indeed by any other physical or biological process.

Such an all-embracing definition is of questionable value. He then goes on to argue that:

A further example relates to the use of the term "gross production", which, for the following reasons, is not a term to be retained.

Conceptually, gross photosynthesis is an unsatisfactory term because the respiration which occurs in the light during photosynthesis is very closely coupled to the photosynthetic process. For example, photorespiration has the same action spectrum as photosynthesis and its rate is linked to the rate of photosynthesis.

Practically, it is unsatisfactory because the plant respiration that occurs in the light concurrently with photosynthesis cannot be measured or reliably estimated on a routine basis. This respiration is therefore usually ignored in production studies. Consequently, for operational purposes, gross photosynthesis or gross production is usually taken as the absolute sum of net photosynthesis in the light and respiration in the dark of the plant or stand. This is not gross production in the sense implied by the use of the word "gross" and in terrestrial C_3 -plants is a considerable underestimation because of photorespiration.

Thus photorespiration is an inevitable consequence of photosynthesis from which it cannot be separated either practically, as an amount, or conceptually, as an independent process. Hence gross photosynthesis and gross production are not viable terms. The continued use of a quantity called gross production, based on an operational definition, might be justified on the grounds of familiarity of usage. However, such usage leads to apologies by the user and confusion of the recipient. Consequently the term should be dropped altogether and any similar, single quantity required should be defined in terms of the rate processes or amounts being summed (e.g., net photosynthesis of leaves + respiration of leaves at night + respiration of non-photosynthetic tissue (stems, roots, etc.) during day and night).

Worthington clearly sees the distinction between operational and fundamental definitions and opts for the former. I shall return to this later. I would, however, disagree with him over the discarding the term gross photosynthesis. My argument is as follows: in the case of microalgae we have gone some way in devising methods for the measurement of light respiration and establishing the scale (e.g., Grande *et al.*, 1989). I would argue that if we are to throw away the concept of gross photosynthesis then we remove the incentive to further develop these techniques, which in the long run will limit our understanding of phytoplankton light relationships. Currently, for example, plankton light-photosynthesis curves are based substantially on ^{14}C -determined production rates; yet the prevailing view is that this technique approximates to net primary production. If so, biochemically the ^{14}C technique, it is not the correct basis for P vs I curves; they would be better based on gross as opposed to net production measurements, if the algal respiration term needs to be removed for modelling purposes it is better done explicitly.

How good are our definitions compared with our methods of measurement?

No doubt I have missed other productivity definitions, and perhaps one ought to consider the literature on terrestrial ecology; however, the preceding should be sufficient to make it very clear that there is no easy consensus to be found. How unsatisfactory the state of affairs is to the experimentalist may be illustrated by putting forward an argument that we are now able to measure plankton production more precisely than we can define it. It runs as follows.

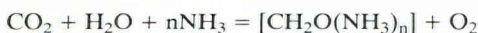
The oxygen technique for the measurement of photosynthesis can achieve an analytical precision (standard error) of about $0.1 \mu\text{mol} \cdot \text{l}^{-1}$ for a typical light-dark bottle measurement involving four replicates. In oligotrophic waters, where rates are in the order of $1 \mu\text{mol O}_2 \text{l}^{-1} \text{d}^{-1}$, this gives a relative analytical error of 7%. In other marine areas, where photosynthetic rates may rise to $5\text{--}10 \mu\text{mol O}_2 \text{l}^{-1} \text{d}^{-1}$, the analytical error will fall to somewhere in the region of 1.5%. The precision of the ^{14}C technique is rarely reported but it is my impression that given good experimentation, the random errors fall in the region 5–10%.

Thus, as a generalization, we may ascribe 5–10% as the order of error for the two major productivity techniques. This is the scale of errors we were able to achieve in oligotrophic waters (Williams *et al.*, 1983; Williams and Purdie, 1991); so, for marine systems generally, this may be conservative.

Let us now consider two widely held definitions of production and their implications on the estimation of production rates. The first definition takes gross primary production as the rate of conversion of light into chemical energy (e.g., Krebs, 1972; Fogg, 1980); the second definition takes production as the rate of carbon fixation (e.g., Cushing *et al.*, 1958). In order to write stoichiometric equations I shall make the simplifying assumption that since oxygen is an early product of the photosynthetic light reaction it may be taken as a measure of the rate of energy utilization. This assumption is not necessary, but it makes the argument more straightforward.

I shall consider the rate of production, according to the above definitions, in the presence of either ammonia or nitrate as nitrogen sources, using Redfield type stoichiometric equations and a photosynthetic product $[\text{CH}_2\text{O}(\text{NH}_3)_n]$, where n is the nitrogen to carbon assimilation ratio ($0 < n < 1$).

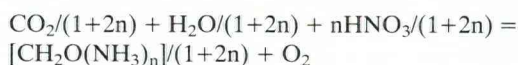
In the presence of ammonia



In the presence of nitrate



If energy (light) is limiting, then the output of oxygen would be constant in either case, thus all the terms in the second equation would be reduced by $1/(1+2n)$, in order to keep the oxygen production rate the same, i.e.,



Thus, under light limiting conditions, a change in the form of inorganic nutrient from ammonia to nitrate would result in a reduction of the photosynthetic rate (if carbon is the form measured) or no change (if oxygen output is measured). Conversely, if the dark reaction, rather than the light reaction were limiting, then a switch from ammonia to nitrate as a nitrogen source would result in no change in photosynthetic rate in the case of carbon-based measurements, whereas oxygen-based measurements would show an increase in photosynthetic rate. In some respects this is the same as saying that the PQ is dependent upon the state of oxidation of the nitrogen source.

The factor $2n$, which originates from the N/C assimilation ratio, represents the uncertainty when comparing the “energy”-related techniques for measuring production and the “carbon”-related techniques. If, for example, light is limiting and the rate of energy assimilation is constant, then if nitrate is the nitrogen source the rate of carbon fixation has to be reduced by $1/(1+2n)$ as compared with ammonia as a nitrogen source to allow for the energy spent on reducing nitrate. If the C/N ratio is 6, then there will be a 25% reduction in the rate of carbon fixation but, of course, no change in the rate of oxygen production. Conversely, if carbon or nitrogen assimilation is limiting, then the difference in nitrogen source will give rise to a 33% increase in the rate of oxygen production with no change in the rate of carbon fixation. If the C/N ratio is 4, then changes would be respectively 33% and 50%.

Both the oxygen and the carbon dioxide technique may be argued to be legitimate methods, yet our definitions give rise to a 25 to perhaps 50% disparity over the photosynthetic rate derived from these methods; this is substantially greater than the analytical error (5 to 10%) associated with the two methods.

Towards a consistent set of definitions

It is very clear that there is no consensus on what constitutes a measurement of planktonic production. As will be evident from the earlier part of this article the definitions fall conceptually into two classes. One set,

which originates from algal physiologists, biochemists, and theoretical ecologists (e.g., Macfadyen, Steemann Nielsen, Krebs, and Fogg) views production as the biochemical injection of energy into the biosphere. The second set comes from community ecologists, modellers, biogeochemists (e.g., Riley, Strickland, Platt) who are concerned with the organism side of production, i.e., yields of groups within the food web, models of material flow within food webs. The former group base their definitions primarily on energy flow, the second on material flow and the argument given above illustrates that this difference in perspective can give rise to significant differences in what is and is not a correct measurement of planktonic production, and as such, ultimately is a limit of the accuracy of our measurement of production.

I had expected, when writing this article, to be able to find a single definition and so bury this confusion. I find that this is not possible, but what I believe one can do is to reduce the variety of definitions.

It seems inescapable that we need definitions at two levels: at a conceptual level and at an operational level. The need for operational definitions is self-evident and probably does not need justifying. I think it is worth putting down the argument for fundamental definitions. Operational definitions will inevitably reflect the technology, more than the concepts, available to field ecologists. For a number of reasons there is a strong element of conservatism amongst ecologists in the techniques that they are willing or able to adopt as a routine for field work. Thus, without some provocation it would be all too easy to define primary production as what is measured with the ^{14}C technique and feel that the problem is solved, and thus reduce the motivation to progress our methodology.

In defining the various production terms, either fundamentally or operationally, we need to do so in the context of the two physiological processes photosynthesis (P) and respiration; also to recognize that the latter can be apportioned between two halves of the planktonic community: algal respiration (R_a), in its various forms, and heterotroph, i.e., microorganism and metazoan (R_h) respiration.

Given this terminology, it is of course simple and conventional to define the long-standing terms as follows:

Gross primary production (P_g) = P

Net primary production (P_{np}) = P - R_a

Net community production (P_{nc}) = P - R_a - R_h

There is a tacit assumption that the system is closed; conceptually it is not difficult, it seems to me, to apply the concepts to open systems (see Platt *et al.*, 1984).

The crux of the problem is the definition of the terms photosynthesis and respiration. The following seem to me to serve as fundamental definitions of the two processes:

Photosynthesis: the conversion of light into metabolic energy

Respiration: the conversion of metabolic energy into heat

These definitions are based on that of Krebs and, particularly, of Fogg. I have chosen to use the term metabolic energy (Platt *et al.*, 1977 have effectively used this approach also) in preference to the more commonly used term chemical energy, because the former is immediate and invokes the necessity of the biochemical process, i.e., it would separate the chemical oxidation of iron or H_2S from the biological respiration of these forms. Very importantly, implicit in this definition is that the reduction of molecules such as dinitrogen, nitrate, and sulphate is as much part of the photosynthetic process as the reduction of carbon dioxide. This is contained in the definition given by Fogg (1980) and it suggests in principle also that the reverse processes, e.g., nitrification should be considered as a component of heterotroph respiration. The separation of chemical oxidation from respiration has one minor consequence – it means that even in a closed system the biological input of energy is not equal to the biological output, because there may be some non-biological release of energy in the form of chemical oxidation.

The definition is based on the concept of free energy, and although free energy as a basis for the construction of food webs has conceptual attractions, in aquatic ecology it has several practical limitations, e.g., how does one measure the free energy of organic material as excreted by microalgae when it is in dilute solution, in a solute of anomalously high specific heat?

Whereas we are not able to measure readily metabolic energy flux directly within the planktonic community we can, however, measure the flux of a number of materials, which brings us to the problem of an operational definition. Many authors (e.g., Riley, Strickland, Odum) refer either directly or by implication, to the production of organic matter or material. As far as I am concerned, we lack a rigorous definition of organic matter (e.g., is urea an organic compound; historically perhaps, although a strong case can be made for the contrary) and we lack convenient methods for its analysis: ashing and dichromate oxidation of collected particulates approach a measurement of organic matter but are not practical approaches for production measurements in planktonic ecology. Thus organic matter itself is not a useful basis of measurement and we need to turn to specific elements that are major reactants and products of the photosynthetic and respiratory processes.

Oxygen may be argued to be a practical surrogate for energy (phlogiston would have been better) being metabolically intimately and inevitably associated with biochemical energy transformation, and one can define production in terms of oxygen, e.g., P_g^O , P_{np}^O , and P_{nc}^O .

There are obvious practical problems if this were to be put forward as the sole basis for an operational definition. Oxygen is really a by-product of photosynthesis and although organic material (or reduced carbon) when it passes through a food web may be viewed as an oxygen debt (essentially the same as the free energy concept), it would be of no practical value in constructing food chain models.

Carbon clearly is the other choice: it is one of the other two major elements involved in the photosynthetic process. The techniques for its analysis are now well advanced and generally more suitable than the third major element – hydrogen. Organic carbon as a basis for production terminology has the disadvantage over oxygen as a product of photosynthesis that the photosynthetic product, organic carbon, occurs in a variety of chemical forms, physical states, and ecological compartments, and therefore greater prescription of the location and nature of the product is necessary.

One may put forward carbon-based definitions for gross, net primary, and net community production as follows:

Gross primary carbon production (P_g^C): is the organic carbon produced by the reduction of carbon as a consequence of the photosynthetic process over some specified period of time.

This would include material that is no longer associated with the autotrophic cell; that is to say, material which may have been excreted and perhaps metabolized by micro-organisms, grazed by the zooplankton, as well as material lost by algal mitochondrial respiration and photorespiration. It would not take into account all the metabolic energy derived from the photosynthetic process, e.g., that put into the reduction of nitrate and sulphate would not be included.

Net primary carbon production (P_{np}^C): is gross primary carbon production minus the losses in carbon due to autotrophic respiration = $P_g^C - R_a^C$ over some specified period of time.

It is particularly important in the case of net production definitions that the time scale is unambiguous; a day can be taken to mean the illuminated period or the whole 24 h period. The loss (respiratory) terms for carbon seem to be fewer than oxygen. Both are probably involved in photorespiration; neither Mehler nor "chlororespiration" are regarded to involve carbon oxidation. It is perhaps significant to note that if Beardall and Raven (1990) are correct in their conclusion that "photo-

respiration in both eucaryotic algae and cyanobacteria is largely suppressed by the activity of a CO_2 concentrating mechanism", then R_a^C would be largely dominated by dark respiration and thus R_a^C (and thus P_{np}^C) is potentially more readily determined from chemical methods than their equivalent oxygen rates.

Net carbon community production (P_{nc}^C): is gross primary carbon production minus all losses in carbon due to respiration = $P_g^C - R_a^C - R_h^C$ over some specified period of time.

This, whether defined in oxygen or carbon terms, has the inherent problem of size scale. In part this was encountered earlier when discussing the equivalence of net and new production. The terms gross primary production and net primary production concern themselves with algal processes, which are for the most part microscopic, and are reasonably well sampled by our *in vitro* procedures. This is not necessarily the case for respiration, which is a component of net community production and in principle includes the activity of all organisms from bacteria to whales. *In vitro* techniques commonly involve sample volumes of the order of 100 cm^3 , which probably reasonably samples organisms up to perhaps 250 to $500\text{ }\mu\text{m}$ in length; in many situations (see, e.g., Williams, 1981; Platt *et al.*, 1984) much of community respiratory metabolism may lie within this size scale and so the errors due to omission of larger forms are perhaps not serious. Longhurst *et al.* (1990), however, argue that the respiration of migrating zooplankton makes a significant contribution to overall zooplankton respiration and so the contribution of these larger forms that would not be sampled by *in vitro* procedures has to be taken into consideration. Following Platt *et al.* (1984), we shall probably need to add the qualifier "small community" to the term.

Conclusion

I have considered a number of definitions of plankton productivity, and from them have attempted to put together an unambiguous and workable set. I have come to the conclusion that we need to continue to use two general forms of definitions – one set based on energy and the other on material, carbon being the appropriate form. As oxygen metabolism is closely associated with energy flux, it may approximate to energy flux. We should note that the photosynthetic flux of material (i.e., carbon) and energy are not linked stoichiometrically; their relative rates of metabolism are controlled by other processes going on inside the cell, e.g., the reduction of nitrate. Our field methods now have sufficient precision to render variations due to these effects significant.

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