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The comparative estimation of phytoplanktonic, microphytobenthic and macrophytobenthic primary production in the oceans ¹

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Abstract

The contributions of the planktonic unicellular algae (phytoplankton), the benthic unicellular algae (microphytobenthos) and the benthic multicellular algae (macrophytobenthos) to the primary production of the world ocean are evaluated, together with the respective limitations regarding data, concepts and methods. The use of "free-water" methods (*e.g. in situ* oxygen or CO₂ budgets) is recommended in complement to the more specific measurements on enclosed organisms. For phytoplankton, a previous estimate of 30 · 10⁹ t C y⁻¹ is retained as a minimal estimate. Earlier estimates of the world benthic production have been based on indirect calculations; revised estimates are suggested here which still lack precision but rely on the actual measurements available at present. Primary production of the micro- and macrobenthic algae amount to 50 and 375 g C m⁻² y⁻¹ respectively as averages for the whole photic layer they can colonize, and total 2.9 · 10⁹ t C y⁻¹ for the world ocean. Thus, benthic algae contribute some 10% of the total marine primary production. On the continental shelf alone, the contributions of benthic and planktonic algae are commensurate and nearly equivalent.

Key words : Global carbon cycle, Macrophytes, Microphytobenthos, Phytoplankton, Primary production.

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Résumé

Contributions du phytoplancton, du microphytobenthos et du macrophytobenthos à la production primaire marine

Trois catégories d'algues sont considérées : les unicellulaires planctoniques (phytoplancton), les unicellulaires benthiques (microphytobenthos) et les pluricellulaires benthiques (macrophytobenthos). Les principales limitations méthodologiques de la mesure de la production primaire dans chaque catégorie sont examinées. L'emploi de méthodes n'impliquant aucune manipulation des organismes (telles que bilans d'O₂ ou de CO₂ *in situ*) est recommandé, conjointement aux mesures expérimentales plus spécifiques en milieu clos. Une évaluation des trois contributions à la production primaire mondiale est proposée. Pour le phytoplancton, on retient l'évaluation récente mais probablement sous-estimée de $30 \cdot 10^9$ t C an⁻¹. Les bilans mondiaux antérieurement proposés pour la production benthique reposaient sur des calculs indirects; on avance ici de nouvelles estimations qui, bien qu'imprécises, se basent sur les données effectivement recueillies jusqu'à présent. Les productions moyennes respectives du micro- et du macrophytobenthos dans l'ensemble des zones photiques colonisables seraient de 50 et 375 g C m⁻² an⁻¹; elles totalisent de l'ordre de $2,9 \cdot 10^9$ t C an⁻¹, soit 10 % environ de la production marine totale. Sur le plateau continental seul, les productions planctonique et benthique sont à peu près égales.

Introduction

If one considers that each of the three types of primary producers included in the title has already lead to an immense (in the case of plankton) or fairly large (benthos) amount of literature consisting of papers, reviews, books and meeting reports, then a paper dealing with the three types all together may seem to be exceedingly ambitious. It may be useful, however, for several reasons, whatever partial and cursory it may be.

The first reason may be called globalism. Obviously, the times are ripe in many fields of the ocean, earth and environment sciences, to systems approaches and global assessments. One of the goals is to answer this question: is benthic production quantitatively significant, on the world scale, as compared to planktonic production? (If not, to which extent is it significant on the continental shelf alone?)

The second reason is related to another modern principle: interdisciplinarity. With few exceptions (which will be reviewed here), phytoplankton, microphytobenthos and macrophytes are studied separately by different specialists using different methods. Yet the three types of organisms share many properties (they all are marine algae; they coexist, apparently, in the same environment, and they may have to compete locally with each other (see the photograph by Huang and Boney (1984) of diatoms destroying the sporelings of a red alga). Several groups of algae, for instance, have colonized both benthic and planktonic habitats, and this even applies to different species of the same genus and, furthermore, to different life stages of the same species. This makes a comparison of adaptative strategies very tempting (see Fryxell (1983) for an introduction). On the other hand, such a comparison may also be of great benefit for the development of the concepts and methods used in production studies, as we do not know of any specialist in her (his) respective field who would not complain about

ambiguities of the concepts and uncertainties of the methods. Our hope is that "looking into the neighbour's garden" may clarify some ideas and help to improve on some strategies.

The modern literature includes a remarkable (still rarely quoted) review of methods and processes pertaining to all the categories of producers in marine and freshwaters (Hall and Moll, 1975) and several reviews devoted more specifically to one or another group of algae (see the relevant section below). As for comparative assessments of benthic vs. planktonic production, only rough estimations have been published.

The objectives of this paper are thus,

— to provide a global estimation of the respective contributions of plankton, microbenthos and macrobenthos to the primary production of the oceans, and to point out the current limitations of such estimates;

— to review the few studies which provide simultaneous measurements on two or three types of producers;

— to compare the three estimates and ascertain their respective contributions to total production.

As the scope of this paper is very large, let us be clear about what will not be found here: (1) neither the concept of primary production, nor the incidence of recycling, excretion, respiration, photosynthetic quotient, duration of the experiments, and significance to further trophic levels will be examined, because each of these points would deserve a proper review or book; (2) specific methodologies will not be discussed, because this has been done elsewhere (as quoted). Up to now, phytoplankton has received the more attention in all respects. As our purpose is to bring the three types of algae into a common perspective, the state of the art about phytoplankton will just be summarized whereas benthic production will be given relatively more attention.

As far as production figures are concerned, the scope of this paper is restricted to the oceans, but methodological and conceptual aspects may include reference to freshwater studies, so that limnologists will hopefully find some interest in the reading. Only photosynthetic production is considered (chemoautotrophy is not). Throughout this paper, "production" is understood strictly as an increase of biomass during a time unit, the term "productivity" being used only when an additional dimension is introduced.

Considering the abundance of the literature to be covered here, we have chosen to focus primarily on recent references; most of the papers that can be called "classical" today will be implicitly included but not quoted.

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Looking for a unifying method

A variety of principles has been applied, up to now, to the measurement of primary production by the three categories of algae considered. As a matter of fact, these principles are so diverse (Table 1) that a common conceptual frame is difficult to

TABLE 1. — Principles used for the measurement of primary production of the algae.

	Phytoplankton		Microphytobenthos		Macrophytobenthos	
	Bottles	Open	Chambers	Open	Chambers	Open
BIOMASS CHANGES						
Weight	—	—	ε	—	?	+
Cell counts	ε	ε	ε ?	—	0	+
Chlorophyll	ε	ε	ε ?	—	—	?
Remote sensing of chlorophyll	0	ε	0	— ?	0	— ?
METABOLIC CHANGES						
<i>External</i>						
Nutrients	ε	ε	ε	—	ε	ε
O ₂	+	+	+	ε	+	+
CO ₂	— ?	ε	— ?	— ?	ε	ε
<i>Internal</i>						
¹⁴ C	+	ε	+	—	+	—
¹⁴ Chlor.	ε	ε	ε	ε	ε	ε

+ largely used; ε seldom used; — not used; 0 not applicable.

establish. By “external” and “internal”, we mean that metabolic changes can be followed either in the surrounding medium (*e.g.*: all the oxygen methods) or in the organisms themselves (*e.g.*: all the ¹⁴C methods). On the other hand, “bottle” and “free water” mean that any application may be practised, at least theoretically, under two ways: enclosing the algae (usually in bottles), or leaving them free in their natural environment. Combining the vertical and the horizontal columns in Table 1, and excluding the cases of non-applicability, we are left with some 50 possibilities. Note that the grid could be extended or subdivided with additional entries; for instance, “mesocosms” could be inserted between “bottles” and “free water”. As the symbols indicate, a given approach may have been widely used, or little used, or not used at all. Different reasons may account for this:

— suitability of the material (*e.g.*: biomass changes are more easily followed in the macrophytes than in other types of algae);

— novelty of the method (*e.g.*: the Redalje and Laws' method (1981) of labelled chlorophyll has apparently not diffused out of the planktologists sphere yet);

— practicability and cost (*e.g.*: avoiding the use bottles in ¹⁴C experiments is possible by pouring directly the isotope into a small lake (Bower *et al.*, 1987, and references therein), but is hardly feasible at sea).

In addition to the grid of what we call here “methods”, one has to choose among the technical possibilities of applying them — what we call here “techniques” (For instance, users of the ¹⁴C method have to decide about a technique for measuring radioactivity). This distinction once being made, there is (1) no general agreement about the

preferably of a given "method", even within one category of algae, and (2) even a standardization of "techniques" for applying a given method to a given category of algae is difficult to achieve.

Clearly, the only common point is that most investigators use the term "primary production"; yet few of them do, in fact, measure the same rate or the same processes. As primary production is a basic property of ecosystems, this state of affairs will have to be improved. Obviously, if a common method is to be found, this should measure the same thing in all cases: hence the choice for a horizontal column in Table 1. Then the common method should measure it in the same way in all cases: hence the choice of a vertical column. A solution to the latter requirement is that organisms should be manipulated as little as possible (this because handling, incubating and analysing procedures differ necessarily for the different types of algae). If considerations of practicability are added, we finally reach the conclusion that oxygen or CO₂-system changes in unenclosed bodies of water are the most promising approaches. This prediction is reinforced by the recent improvements in the analysis and continuous monitoring of the relevant parameters. A provision should be made, however, for unpredictable advances in chemical techniques that would allow precise and continuous recording of low nutrient concentrations, and for sudden advances in remote sensing technologies.

This does not mean at all that bottles are becoming obsolete, as they must still be used whenever the specific production of a given organism or population or water mass is to be measured and/or compared to another. Furthermore, the "bottles" and "free-water" approaches are, obviously, complementary.

An overview of phytoplankton production

Because of the poor precision and reproducibility which can generally be obtained when estimating phytoplankton biomass, the attempts to measure production by following changes in biomass have never been generalized, even when they have proved successful. This approach has been practised by means of various techniques: cell counts (Riley, 1952), electronic particle counting (Cushing and Nicholson, 1966), or chlorophyll measurements (Saijo *et al.*, 1969), and is certainly not abandoned today (Olivieri and Hutchings, 1987; Sheldon and Rassoulzadegan, 1987). As sampling error is particularly critical in plankton studies, bottles have generally been preferred to "open water" approaches. Both approaches represent the more direct way of estimating net production. The data are so limited, however, that they cannot be used to estimate global productivity.

Global estimates from the ¹⁴C data

All measurements of phytoplankton production have been obtained through a metabolic approach, which offers a wide choice of methods (Table 1). Among the latter, as is well known, the ¹⁴C method has been employed so extensively that

oceanographers were lead in the late 60's, to revise the earlier assumptions derived from some oxygen measurements by G.A. Riley or H.U. Sverdrup, and to compute the total primary production of the world ocean. The milestone paper of that time is Ryther (1969). It was then admitted that the net primary production of the oceans amounts to $20\text{-}30 \cdot 10^9$ tons of carbon per year (Koblentz-Mishke *et al.*, 1970; Platt and Subba Rao, 1975), and this estimate is still used in ecology and biogeochemistry. There are several biases, however:

— Several other estimates have been successively derived from the above estimate. They rely on one another and gained much of their credibility through repetitivity. The source data, in so far as they are known, would certainly need to be revisited (Koblentz-Mishke, for instance, made use in her calculations of "indirect" data and extrapolations of her own).

— The dogma that most of the oceans consist of biological deserts is no longer accepted, on the account that high photosynthetic gross rates and high turn-over rates have been measured there (Sheldon and Sutcliffe, 1978; Eppley, 1980; Jenkins, 1982; Laws *et al.*, 1984, 1987). Although controversy may persist for sometime, it is now recognized that variability in space and time is not less in the centre of the oceans than elsewhere. Platt and Harrison (1985) pointed out that undersampling tends to underestimate, rather than overestimate production.

— In counterpart, the fertility of the antarctic areas has long been overestimated on the account of some high rates that had been obtained in bays in the more favourable season. Clearly, the annual production of neritic waters is about as high in the Antarctic as elsewhere in the world (*e.g.* Whitaker, 1982), but oceanic productivity on an annual basis has to be severely revised downwards (Jacques and Minas, 1981; El-Sayed, 1984). Note that, conversely, the productivity of arctic phytoplankton has to be revised upwards, but this will not affect significantly the global picture (Subba Rao and Platt, 1984).

— Metal contamination has been shown to take place in routine measurements (Carpenter and Lively, 1980; Fitzwater *et al.*, 1982; Gieskes and Kraay, 1984), hence the need for "clean methods". Bottle effects, which had been suspected by earlier workers to affect measurements, have been found to be dramatic by Gieskes *et al.* (1979) and negligible by others. Confinement in small bottles probably reinforces the effects of contamination (Gieskes and Kraay, 1984). Underestimation of production is therefore generally suspected.

— A debate was raised in the early years of the ^{14}C era as to whether gross or net production is measured. This debate is still open today, in spite of the evidence that the ^{14}C method is not able to discriminate between photosynthesis and respiration. Obviously, the rates tend to be net ones when the incubation period is approaching (or exceeding) the generation time of phytoplankton; long incubations introduce various biases, however, and the regulation of growth rate is a complex one. The question may thus be just insolvable.

— Various technical biases may alter the production estimates and their comparability. The reviews by Carpenter and Lively (1980), Peterson (1980), Sakshaug (1980), Colijn *et al.* (1983), Leftley *et al.* (1983) and Gieskes and Kraay (1984) may be consulted on this respect.

Altogether, a consensus is going to be reached that $20\text{--}30 \cdot 10^9$ tons C y^{-1} is an underestimation (De Vooys, 1979; Carpenter and Lively, 1980; Eppley, 1980; Peterson, 1980; Gieskes and Kraay, 1984). We agree, but dare not to say how much this figure is to be raised; a conservative estimate of $30 \cdot 10^9$ t C y^{-1} will thus be retained here.

The alternatives to the ^{14}C method

Much effort has been devoted until recently to comparative measurements of phytoplankton photosynthesis by the oxygen light-and-dark bottle method and the ^{14}C method — as if one of them should be right and the other be wrong. It is now admitted, at last, that each method has its own advantages and limitations and that, given experimental care, both may reasonably agree (Williams *et al.*, 1983; Gieskes and Kraay, 1984; Bender *et al.*, 1987). Consideration of the photosynthetic quotient (and its dependence on the type of nitrogenous source) is particularly relevant (Williams *et al.*, 1979).

As a matter of fact, the controversy has instead turned to the comparison of ^{14}C measurements with production estimates derived from oxygen changes of the unenclosed medium. The latter may consist of either oxygen budgets in the water mass, corrected or uncorrected for diffusion and advection (Sournia, 1968 and references therein); (Gieskes and Kraay, 1984) or vertical fluxes with reference to the Redfield's ratios (Broenkow, 1965; Minas *et al.*, 1986). This is a vast subject with too broad implications on chemical and physical oceanography to be developed here. It should suffice to say that estimates obtained by this "open-sea" approach prove to be the higher and that a vivid debate arose (Shulenberger and Reid, 1981; Platt, 1984; Platt and Harrison, 1985).

For several reasons, the open-sea approaches may supersede Steemann Nielsen's method in the future: (1) the current interest, in international programs, to water column fluxes and biogeochemical budgets; (2) the refinement of analytical procedures for Winkler titration (Bryan *et al.*, 1976) and fine-scale oxygen monitoring (Atkinson *et al.*, 1987), pCO_2 monitoring (Copin-Montégut, 1985), nutrient traces (Garside, 1982) and pH (Fuhrmann and Zirino, 1988); (3) the long-lasting suspicion about the ^{14}C method, in spite of its sensitivity and practicability.

Production, in the proper sense, can be evaluated through remote sensing under three different ways: (1) entering surface chlorophyll measurements into a photosynthetic model (Smith *et al.*, 1982; Platt, 1986); (2) deducing production rates from successive measurements of surface chlorophyll (Dupouy and Demarcq, 1987); (3) measuring the passive fluorescence of chlorophyll (Topliss and Platt, 1986). None of these approaches has been applied to benthic communities yet.

A review of microphytobenthic production

The term microphytobenthos includes here all the unicellular algae living in or on an inert substratum in aquatic environments. Ice algae are included but the epiphytes

growing on macroalgae or phanerogams will be considered together with the latter, for reasons of convenience. As compared to planktonic algae, and to macroscopic "algae" in the common sense, this category has long been neglected. The last fifteen years gave rise to an outburst of ecological, physiological, taxonomical and production studies but production on the world scale has not been estimated yet. We will first discuss the validity of the concepts and the comparability of the results.

Specific methodological problems

The derivation of production from successive measurements of biomass is generally more difficult with microphytobenthos than with the other algae (Admiraal *et al.*, 1983) and authors such as Wetzel (1965) give only relative values. Microdistribution is particularly critical and depends on the space scale in question (Plante-Cuny, 1978; Plante *et al.*, 1986). The correlation between production and biomass may be found to be positive (Cadée and Hegeman, 1977) as expected, but is, at times, not significant (Charpy-Roubaud, 1988). Another drawback is that chlorophyll measurements are particularly liable to interferences among pigments (Varela, 1982); the use of HPLC techniques is much promising (Riaux-Gobin *et al.*, 1987) but it can hardly be extended to routine analysis.

The bulk of production data on microphytobenthos has been obtained through photosynthetic measurements. Both the oxygen (*e.g.* Pomeroy, 1959; Pamatmat, 1968; Sournia, 1976 a, b and c; Es, 1982; Charpy-Roubaud, 1988) and the ^{14}C methods (*e.g.* Grøntved, 1960; Steele and Baird, 1968; Marshall *et al.*, 1973; Cadée and Hegeman, 1974, 1977; Colijn *et al.*, 1983) have been and still are employed. The latter method, which provides figures in terms of carbon directly, may have been the more widely used (Plante-Cuny, 1974) but this may not hold true in the future. The $^{14}\text{C}/\text{O}_2$ alternative may be put in the following terms when applying to microphytobenthos:

— a specific advantage of ^{14}C lies in the possibility of measuring production in air, thus in temporarily emerged communities (Darley *et al.*, 1976; Holmes and Mahall, 1982; Whitney and Darley, 1983).

— In all the ^{14}C procedures, the substrate and the microalgae have to be manipulated and disturbed to some extent (see the review by Plante-Cuny, 1978). The natural environment being thus modified, the resulting rates are, at the best, somewhat virtual, if not "potential" rates.

— As biomass is more concentrated than in the case of phytoplankton, sensitivity is not limiting; then ^{14}C loses its advantage over oxygen. Furthermore, oxygen electrodes offer the possibility of continuous monitoring (see Langdon, 1984, for a recent improvement); and the high resolution permitted by microelectrodes have eliminated most of the artifacts caused by air bubbles within the sediment (Revsbech *et al.*, 1981; Revsbech and Jørgensen, 1983).

Broadly speaking, environmental gradients are much more acute for benthic microalgae than for the planktonic ones, and this may alter the representativeness and the comparability of the results. The euphotic layer here is a matter of centimeters or even millimeters thick (Taylor and Gebelein, 1966; Fenchel and Staarup, 1971; Colijn, 1982) and vertical migrations are common (Harper, 1977; Riaux 1982; Colijn, 1982).

Interactions of light and temperature are complex (Colijn and Van Buurt, 1975; Redalje and Laws, 1983). Other determining factors include the particle size, (Plante-Cuny, 1978; Davis and McIntire, 1983) and hydrodynamics (Amspoker and McIntire, 1978; Admiraal, 1984; Plante-Cuny and Bodoy, 1987). Photoinhibition may be more dramatic than for planktonic algae (Colijn and Van Buurt, 1975; Whitney and Darley, 1983), but sometimes does not take place at all (Charpy-Roubaud, 1988). Wet sediments exposed to air have shown higher photosynthetic rates than immersed sediments (Holmes and Mahall, 1982). Seasonal variations may be considerable (Pamatmat, 1968; Riaux, 1983; Bodoy and Plante-Cuny, 1984) and culminate, as expected, under high latitudes (Matheke and Horner, 1974); annual variations (from one year to another) are still poorly understood (Cadée and Hegeman, 1974). The consequences of inadequate sampling in space and time have been discussed by Asmus (1982) and Shaffer and Onuf (1985).

In view of these and other methodological difficulties (see also Hunding and Hargrave, 1973; Boynton *et al.*, 1981; Shaffer and Onuf, 1983; Varela, 1985; Charpy-Roubaud, 1987), all we can reasonably do is to provide estimates for the microphytobenthic production within orders of magnitude.

Results on the world scale

On the world scale, microphytobenthic production has been preferentially measured in (1) soft-bottom substrates, (2) shallow depths and (3) temperate latitudes. In other words, any attempt to evaluate the global production is at present biased by the scarcity of data originating from hard bottom, from areas beyond the intertidal zones and from low and (particularly) high latitudes. Reviews have been provided by Plante-Cuny (1978, 1984) and Charpy-Roubaud (1987); the two former reviews include extensive tables which summarize the techniques used and the results obtained throughout the world.

The figures themselves, in so far as they have been expressed in comparable units (such as g O_2 or $\text{g C m}^{-2} \text{ year}^{-1}$), are widely scattered. It cannot be said to which extent this is due to natural variability or to the diversity of the experimental procedures. The mean values, however, are often commensurate with each other, particularly if intensive series of data are available (*e.g.*: Pomeroy, 1959; Pamatmat, 1968; Marshall *et al.*, 1971; Joint, 1978). Summaries or reviews have been provided for the temperate seas by Colijn *et al.* (1983), Davis and McIntire (1983) and Hargrave *et al.* (1983). Two recent reviews deserve particular mention here as they provide global figures: Plante-Cuny (1984) suggests $30\text{--}180 \text{ g C m}^2 \text{ year}^{-1}$ for the intertidal, temperate sediments and a mean of $128 \pm 50\%$ (same units) is indicated by Rizzo and Wetzel (1985) for the intertidal zone, regardless of the latitude and substrate. We believe that the latter figure is overestimated. After reexamining the original data and including some others (Grøntved, 1962; Gargas, 1972; Riznyck *et al.*, 1978; Es, 1982), we found it reasonable to suggest the mean figure of $100 (20\text{--}220) \text{ g C m}^{-2} \text{ year}^{-1}$ for the temperate and shallow environments.

Data from tropical seas, although less numerous, and often lacking a full annual coverage, are consistently higher; particularly high production values have been recorded in soft-bottom sediments of coral reefs (*e.g.* Sournia, 1976 b; for reviews, see Plante-Cuny, 1984 or Charpy-Roubaud, 1988). A figure of 66 g C m^{-2} per year in the vicinity of Madagascar (Plante-Cuny, 1978) is noteworthy, as it extends to relatively deep waters (5-60 m) and covers a full annual cycle. A production of $300 \text{ g C m}^{-2} \text{ y}^{-1}$ may be retained for the intertidal tropical parts of the world as a whole (Plante-Cuny, 1984).

The production of benthic microflora decreases towards the higher latitudes, in so far as the number of data (which also decrease in the same way) may indicate it. A tentative figure of 5 g C m^{-2} per year was suggested by Plante-Cuny (1984). Another category of primary producers is to be taken in consideration, however, at these latitudes. These are the complex and diverse microalgal communities associated with ice (Horner, 1976; Fogg, 1977; Hsiao, 1980) and which may not be called properly neither planktonic nor benthic. They may reach considerable biomass at their blooming season and can be extremely shade-adapted. Regarding their production, Fogg (1977) and Subba Rao and Platt (1984) have reviewed antarctic and arctic data, respectively and jointly suggested a production of $10 \text{ g C m}^{-2} \text{ y}^{-1}$ for the "young ice". The latter authors make a reservation about the presumably higher rates to be found in the bottom sea ice. In fact, recent works indicate that this component is more or much more important than previously thought (Horner and Schrader, 1982; Palmisano and Sullivan, 1983; Grossi *et al.*, 1987; Kottmeier and Sullivan, 1987). In the comprehensive study by Horner and Schrader (1982), ice algae accounted for 2/3 of total production, phytoplankton provided 1/3 and the contribution of benthic algae was negligible; the figure of $0.7 \text{ g C m}^{-2} \text{ y}^{-1}$ for ice algae was said to be underestimated for technical reasons.

Altogether, microalgal production of the high latitudes on an annual basis may be only slightly less than microphytobenthic production in the temperate seas at similar depths. As tropical figures are generally higher, we may content ourselves with an overall estimate of $100 \text{ g C m}^{-2} \text{ y}^{-1}$ for the microbenthic primary production in shallow waters of the world ocean.

A review of macrophytobenthic production

We consider in this section the benthic macroscopic algae and include the free-floating sargassoes but we omit the higher plants of all kinds such as seagrasses, mangroves and the salt marsh communities. The reason is that we felt it preferable to deal with algae only.

Specific methodological problems

The methods and, to some extent, the concepts used in production studies differ here in many respects from the two preceding cases. This is related to the truism that macrophytes are large, pluricellular organisms. Compared to planktonic or benthic

microalgae, a number of additional difficulties arise (Littler and Arnold, 1980), and this also makes it difficult to bring the two sets of data into a common perspective:

1. Specific to macrophytes is the choice of a destructive (De Wreede, 1985) or non-destructive method (Littler and Littler, 1985 b). The former seems to be preferred for biomass estimations whereas the latter would be more suitable for production studies, but a general agreement has not been reached yet.

2. As the different parts of a macrophyte grow and metabolize at different rates, the choice of a representative part will pose a problem for the larger organisms (Hatcher, 1977; Drew *et al.*, 1982). Growth and physiological characteristics are also strongly dependent on the season (Williams *et al.*, 1979; Tijssen and Eijgenraam, 1982).

3. Production rates depend also on the shape of the thallus (Littler, 1980 a and b; Morrissey, 1985).

4. Macrophytes are usually a substrate for unicellular epiphytes such as diatoms; this community, in turn, is highly variable under all respects (Cattaneo and Kalff, 1980).

5. When the oxygen method is used, biases arise from the presence of gaseous systems which may store significant amounts of oxygen (McRoy and McMillan, 1977; Zieman and Wetzel, 1980). This effect should be taken into account when the ^{14}C method is used, according to Plante-Cuny and Libes (1984).

Then, as with microphytes, macrophytic production can be deduced either by following the biomass changes or measuring a metabolic rate. Both approaches have been widely used; general reviews are provided by Vollenweider (1969), Plante-Cuny and Libes (1984), Littler and Littler (1985 a) and Lipkin *et al.* (1986).

The parameters for biomass include wet weight, dry weight, chlorophyll content, and length. As all of them are currently in use, comparisons are rarely feasible. Although wet weight is the more commonly used, it is not the more reliable, because of the variability of aqueous content and retention (De Wreede, 1985); for this and other reasons, wet and dry weights are not linearly correlated (Brinkhuis, 1985). When dry weight is used, care is still to be taken as regards seasonality (Mann and Chapman, 1975) and sampling or subsampling procedures (Buesa, 1977; Green, 1979; Littler, 1979, 1980 a, b and c). Another subtlety, which is not relevant to microalgae, is: "standing stock", the quantity of algae present at a given time, is to be distinguished from "standing crop", the repeatedly harvestable biomass (see De Wreede, 1985). Both lead to net productions.

Metabolic rates are measured by the oxygen or the ^{14}C methods. As sensitivity is generally not a constraint for measurements on the macrophytes, the oxygen method may be preferred for the sake of simplicity (and the possibility of flow-through monitoring). Its main disadvantages lie in (1) the presence of the gaseous spaces which may lead to underestimates (see above), an effect which is felt as negligible by Lindeboom and De Brée (1982), however; (2) the frequent occurrence of bubbles in the incubation flasks (Buesa, 1977; Littler, 1979). The ^{14}C methodology is supported by Kremer and Markham (1979), Littler and Arnold (1982) and others but several disadvantages have been pointed out by Littler and Arnold (1985). There is a general agreement that the ^{14}C measurements tend to be lower than those based on oxygen (for a review, see Lindeboom, 1983).

"Flow methods" are particularly suitable for measurements in shallow and productive waters. They have been extensively used in macrophyte studies (coral reefs areas in particular). Descriptions of the methods may be found in the manual edited by Stoddart and Johannes (1978) or in the shorter reviews by Sournia (1982) and Kinsey (1985) and relevant results are included herein (Table 2).

As was the case with microphytobenthos, the production of macrophytes has been preferentially measured, up to now, in shallow waters and in the intertidal range. Measurements at depth or at a distance from the shore are exceptions (Gargas, 1970; Mann, 1972; Towle and Pearse, 1973).

The contribution of epiphytes

Many of the production measurements of the macroalgae implicitly include the production of unicellular epiphytes. In some experiments, however, epiphytes were removed from the samples, and some authors have measured the two rates separately. The more detailed studies on epiphytes deal with the seagrasses. The contribution of microalgae proved to represent a significant fraction of the macrophytic production, in spite of their much lower biomass (Penhale, 1977; Capone *et al.*, 1979; Libes, 1986; Libes and Boudouresque, 1987); it may also exceed phytoplankton production by one order of magnitude (Rodgers and Harvey, 1976). Correspondingly, high turn-over rates were found by Panayotidis and Giraud (1981). In a study by Libes *et al.* (1983), the relative contribution of the epiphytes proved to be remarkably constant throughout the year, because the dramatic seasonal variations exhibited by the macro- and the microphytes were parallel to each other.

Results on the world scale

Table 2 summarizes most of the relevant data expressed in terms of g C m^{-2} per day or per year. We have omitted a number of data about such tropical genera as *Acanthophora*, *Caulerpa*, *Dictyota* and *Halimeda*, the production of which is usually expressed with reference to dry weight. There are indications, however, that these are among the most productive algae of the world (Hillis-Colinvaux, 1974).

The general picture is that macrophytic production is higher than microphytobenthic production by several times and higher than plankton production by one order of magnitude. An overall range of $500\text{-}2,000 \text{ g C m}^{-2}\text{y}^{-1}$, as given by Mann (1973, 1976, 1982) and Mann and Chapman (1975) will be retained here. We are not aware of any previous estimate of the world production that may be attributed to macrophytes specifically; attempts which are more or less relevant refer to such heterogenous categories as "algal beds and reefs" or "nearshore waters" (see the last Section).

TABLE 2. — Primary production of macroalgae, including earlier reviews.

Regions. Zones and Substratum	Genera	Net production		References
		$\text{g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$	$\text{g C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$	
Temperate, subtidal, subarctic rocky shores	<i>Laminaria</i>	3 - 9		Bellamy <i>et al.</i> , 1968
				Bellamy <i>et al.</i> , 1973
		2		Mann, 1973
			600-1750	Mann, 1972
			400-1900	Westlake, 1963
			1330	Field <i>et al.</i> , 1977
			1225	Bellamy <i>et al.</i> , 1968
			120 *	Johnston <i>et al.</i> , 1977
			1000	Mann, 1982
			1000-2000	Mann and Chapman, 1975
	<i>Macrocystis</i>	0.5 - 7		Towle and Pearse, 1973
				Littler and Muray, 1974
			350-1500	Wheeler, 1978
			800-1000	Mann, 1982
Temperate, subarctic, intertidal	<i>Fucus</i>	1.7 - 20		Mann and Chapman, 1975
				Blinks, 1955
				Kanwisher, 1966
		1.3		Breton-Provencher <i>et al.</i> , 1979
		12		Littler and Muray, 1974
Tropical, free algae (water column)	<i>Sargassum</i>		500-1000	Wassman and Ramus, 1973
			2250	Mann and Chapman, 1975
Coral reef, hard substratum	Several genera of <i>Corallinaceae</i>	0.2 - 1		Wanders, 1976 b
				Wanders, 1976 a
				Morrissey, 1985
				Marsh, 1970
				Littler, 1973
				Vooren, 1981
Coral reef, hard substratum, sand	<i>Halimeda</i>	5.7		Hawkins and Lewis, 1982
		2.3		Littler, 1974
Algal flats or algal crests of coral reef	Coralline communities	1 - 5 **		Hillis-Colinvaux, 1974
				The works of S.V. Smith, J.A. Marsh Jr, D.W. Kinsey, reviewed by Lewis, 1977 and Sournia, 1977

* Nutrients limitation. ** Flow method.

Comparative measurements in the field

Obviously, the methods and the experimental procedures usually differ among authors and depend on the type of organisms considered. This is severely prejudicial to comparisons. It is tempting, however, to compare the production rates that may have been obtained simultaneously on two or three of the different plant communities — in so far as consistent units, such as: $\text{m}^{-2} \text{y}^{-1}$, were used.

Macrophytobenthos and phytoplankton

The paradigm here lies probably in the study of St. Margaret's Bay (Canada) using a submarine and scuba diving along 50-km transects (Mann, 1972, 1973). Averaged over the 128 km² of the bay, annual macrophytic production was 3 times higher than that of the water column. A similar trend was noted by Newell *et al.* (1982) in another kelp environment. Gargas (1970) and Cadée (1980) observed also a predominance of the macrophytic component nearshore, with a reversal when depth or distance from the coast are increasing. In counterpart, other authors who compared the primary production of various algae found macrophytes to be of minor importance in some cases (Cadée and Hegeman, 1974; Wetzel, 1965; Plante-Cuny, 1977).

Microphytobenthos and phytoplankton

This is the aspect under which comparisons are the more numerous. As might be expected, the relative contributions of benthic and planktonic algae tend to equal each other at some distance from the coast but this distance is highly variable depending on latitude and environments.

As far as surface or shallow waters are considered, a dominance of microbenthic production is usually observed (Matheke and Horner, 1974; Cadée, 1980; Warwick *et al.*, cited in Field, 1983; Varela and Penas, 1985; Plante-Cuny and Boday, 1987); the more dramatic ratios (up to 50:1) have been noted for coral reefs and atoll lagoons (Sournia, 1976 a; Sorokin, 1973). On one occasion, microphytobenthic production has been found to be relatively negligible, even at the 0.5 m depth (Gargas, 1970). Equivalent rates were noted by Pomeroy (1960), Cadée and Hegeman (1974).

There have been few attempts to evaluate what may be called the "equivalency depth" because, as was said in a preceding section, benthic measurements become rather scarce at depth. No generalization can be made at this stage; equivalency depths of 2 to 40 m have been obtained (Pomeroy, 1960; Cadée, 1980; Charpy-Roubaud, 1988).

Phytoplankton vs. phytobenthos on the world scale

Cautionary notes

Each of the above estimates has limitations of its own. The plankton data are the more abundant and relatively well distributed in the world ocean; more annual cycles in the less productive areas would be welcome, however, and the coverage at the small or middle scales of space and time may be improved. Clearly, the major problem about phytoplankton lies in the understanding of the basic concepts. Seemingly, after having measured primary production extensively for forty years or so, oceanographers still wonder about the significance of "primary production". In fact, their concern about this is much deeper than when they began. Various reserves and doubts repeatedly arise that may be summarized under three queries: how much carbon is recycled during the course of the experiments? How much organic matter is taken or rejected in the medium during the experiments? What are the effects of enclosing plankton in bottles? More efforts are devoted at present to solve these problems than to gain new data from unknown regions.

The situation is quite different with microphytobenthos which has been, roughly speaking, neglected. Biomass and production have been measured at relatively few localities which are preferentially shallow, temperate, and easily reached from a marine laboratory. Thus, the extent and importance of microphytobenthos on the outer parts of the continental shelf are virtually unknown. The qualitative composition is largely ignored as well, except for the diatom component. Microphytobenthos is frequently a kind of "crypto-benthos" to the human eye, although attention has long been called to coloured patches on the sand. The ubiquiteness of microalgae on any aquatic substrate is unsuspected to many — unless they have not read Sieburth's "*Microbial seascapes*" (1975).

The knowledge of macrophytic production suffers from the same limitations with regard to world distribution of the data. In addition and opposite to the latter category, bias may have arisen from the macroscopic nature of these algae, as so-called representative samples and attractive populations have obviously been selected preferentially. Thus, more measurements are available for kelp beds than for less conspicuous algae. On the other hand, the methods are more diversified, and many of them rely on growth measurement or biomass changes throughout one season, so that the production figures tend to be more "net" than the presumably net rates measured on the other communities.

Both the micro- and macrobenthic production may be underestimated for a common reason. Few measurements are carried out in air, although the ^{14}C methods makes it possible; yet photosynthesis has been shown to be more intense on emersed populations of microalgae (Holmes and Mahall, 1982) and macroalgae (Johnson *et al.*, 1974).

Obviously, phytoplankton, microphytoplankton and macrophytes differ from each other in their morphological and functional characteristics. *In situ* comparisons of light adaptations are too few (Gargas, 1980; Rivkin and Putt, 1987) to allow any generalization. On the other hand, benthic algae are probably better adapted for

assimilating nutrients at low concentrations in turbulent waters; analyses of their C/N/P ratios showed them to be relatively nutrient-depleted, however (Atkinson and Smith, 1983) if the additional carbon contained in cell walls and intercellular matrix does not allow for the anomalously low C/N/P ratios. This stands rather as a paradox that considerations of kinetics and turnover should try to elucidate.

Previous estimates

Previous reviews of primary production in the world ocean generally include only a few lines about benthic production and they are all unclear about the reference rates, the surface area and the kinds of organisms or environments under consideration; an exception is the more detailed account given by De Vooy (1979). Some quotations follow, starting with the now classical papers by Ryther (1969) and Koblentz-Mishke *et al.* (1970). The latter two do not mention benthos at all. Relying on a previous estimate of 450,800 km for the total length of coastlines and considering that the benthic photic zone extends to some 1-10 km from the coast, Bunt (1975) calculated that an area of $0.45\text{--}4.5 \cdot 10^6$ km² is available for benthic photosynthesis; then, on considerations of the radiation available, he hypothesized an annual production of $0.65\text{--}6.5 \cdot 10^9$ tons C, which would amount to 2.8-28% of the (then) "current assessment of $23 \cdot 10^9$ tons for the world ocean". Whittaker and Likens (1975) in their biosphere budget considered a category of "algal beds and reefs" which would account annually for $1.6 \cdot 10^9$ tons of dry matter out of a "total marine" of 55 in the same units (that is: 2.9%). These authors also considered a category of "estuaries, excluding marsh" which may include some benthic production. A contribution of 0.5% of the ocean surface, 67% of the algal biomass, and 7% of marine production is attributed to macrophytes by Whittle (1977) on the account of data allegedly taken from Whittaker and Likens (or from elsewhere?). Based on the same source, Smith (1981) retained an area of $2 \cdot 10^6$ km² and a macrophytic production of $1 \cdot 10^9$ tons per year of 5% of the oceanic production. De Vooy (1979) calculated the contribution of "kelps" and "other weeds" separately, on the consideration of the respective lengths of coastlines they represent; the sum is only $0.03 \cdot 10^9$ tons C y⁻¹, *i.e.* only 0.06% of the total aquatic production, freshwaters included. The contributions of seagrasses and marshes were also evaluated, "benthic diatoms" being mentioned but not evaluated globally. The resulting composite, non-phytoplankton category would eventually be responsible for 3.8% of the total production (De Vooy, 1979).

A revised estimate

We may do better today than using such extrapolations. Quantitative measurements on micro- and macrophytobenthic populations have become available in sufficient number and in sufficiently diverse areas to allow a first calculation to be made, even if approximate and provisional (Table 3). The main limitation lies in the dramatically decreasing number of data with increasing depth or increasing distance from shore. A simple though reasonable approach is to evaluate mean production and to multiply by the respective areas.

TABLE 3. — World estimates of marine primary production.

	Phytoplankton	Microphyto- benthos	Macrophyto- benthos ¹
World area available 10 ⁶ km ²	362	6.8	6.8
Range of production g C m ⁻² y ⁻¹	50-300	20-300	500-2,000
World production 10 ⁶ t C y ⁻¹	≥30	0.34	2.55 ²
Production of continental shelf	4	0.34	2.55

¹ Omitting higher plants, the production of which has been estimated as $0.49 \cdot 10^9$ t C y⁻¹ by De Vooy (1979).

² Accounting for their patchy distribution.

Estimates of the total area of the world ocean available to benthic algae, under the various terms of "inshore waters", "coastal areas", and so on, differ widely among authors; a range of 0.45 to $49.4 \cdot 10^6$ km² was found in a set of six references (Ryther, 1969; Koblenz-Mishke *et al.*, 1970; Bunt, 1975; Platt and Subba Rao, 1975; Whittaker and Likens, 1975; Smith, 1981). We prefer to consider that the 0-200 m range covers $27.123 \cdot 10^6$ km², that is: 7.49% of the world ocean (Menard and Smith, 1966) and that a mean benthic photic zone of say 50 m represents one fourth of this area ($6.8 \cdot 10^6$ km² or $6.8 \cdot 10^{12}$ m²).

Microphytobenthic production in the intertidal areas and shallow environments is about 100 (20-300) g C m⁻² y⁻¹, depending on latitudes, seasons and substrate, as was detailed above. A mean annual value of 50 g C m⁻² is assumed for the entire 0-50 m fringe. Admitting that microphytobenthos colonizes this entire zone, its world production would be:

$$50 \cdot 6.8 \cdot 10^{12} \text{ g} = 0.34 \cdot 10^9 \text{ t C y}^{-1}$$

As for the macrophytes, which produce annually 500-2,000 g in the intertidal and subtidal areas, an average of 750 g may be suggested for the 0-50 m zone. The geographical coverage of this zone by macrophytes is obviously uneven, however, and the above range is biased by the high values originating from "macrophyte-dominated ecosystems" (Mann, 1982; Field, 1983). Applying a correction factor of 50% the world production of macrophyte algae would be:

$$750 \cdot 0.5 \cdot 6.8 \cdot 10^{12} \text{ g} = 2.55 \cdot 10^9 \text{ t C y}^{-1}$$

The highly productive coral-reef waters, the area of which represents up to one tenth of the benthic photic zone (*e.g.*: $617 \cdot 10^3$ km², in Smith, 1978), may pose a problem: their macrophytic and microphytobenthic contributions are included in the above estimates, but the role of symbiotic zooxanthellae is not (the net production of the coral/algae association is low or nil, however, in spite of a high gross production). Although seagrasses have been omitted here, let us mention that "production values of 500-1,000 g C m⁻² y⁻¹ are "typical for the seagrasses" (Zieman and Wetzel, 1980), and that De Vooy (1979) ascribes a world production of $0.49 \cdot 10^9$ t C y⁻¹ to the category "angiosperms".

In comparison with the (presumably underestimated) $30 \cdot 10^9$ t C produced annually by phytoplankton (Table 3), two conclusions arise:

(1) Production of benthic algae amount to about one tenth of the world's marine primary production, and this is about twice the recent estimates by Whittle (1977), De Vooy (1979), or Smith (1981). Although we tend to think that such a percentage is worth consideration by itself, the issue may depend on the use which is ultimately made of the global estimates (for instance, the long-term predictions about geochemical budgets usually imply errors higher than 10%).

(2) Considering the continental shelf only, one fourth of which is assumed here to have a significant phyto-benthic production, this production nearly equals that of phytoplankton of the whole continental shelf, say $4 \cdot 10^9$ t C y^{-1} (see Ryther, 1969: "coastal zone" = $3.6 \cdot 10^9$; Platt and Subba Rao, 1975: "shelf" = $4.057 \cdot 10^9$, same units). Comparative measurements in various localities confirm the global estimates on this respect. This had been suggested on an hypothetical basis by Ryther (1963) but has been generally overlooked since. As a consequence, benthic and planktonic productions should deserve equal attention in coastal and shelf studies.

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