

PRIMARY PRODUCTION IN COASTAL LAGOONS

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1. Introduction

The expressions *primary production* and *productivity* have been used indiscriminately in aquatic environments, even to the extent of using the same measuring units, with some minor differences. According to Wetzel (1975) production is the weight of new organic matter formed in a period of time per volume or area, plus losses due to respiration, excretion, secretion, damage, death, or grazing. It is also the increase in biomass in a given time. Primary productivity is the potential rate of biomass addition per time per area; this term implies an average instantaneous rate per hour, per day, or per year. These two concepts have been confused with biomass, which differs basically in the units: biomass is not a rate, but it is the weight of plant and animal matter in a given area; hence, it can be expressed in g/m^2 , g/m^3 , or volume displaced per liter.

The primary producers, photosynthesizers or autotrophic organisms of aquatic environments encompass microscopic organisms (phytoplankton), macroalgae, and phanerogams (from very small free-floating plants to large trees, such as mangroves). They all participate in inorganic carbon assimilation to produce organic carbon at diverse rates.

Although, published data on primary production and/or productivity in coastal lagoons has increased in the last years, their interpretation still poses a problem since many studies have focused mainly on the description of the most relevant producing populations.

Primary production in coastal lagoons can be dominated by phytoplankton, benthic micro- and/or macro-algae, macrophytes, and, in special cases, by a combination of all of them. The afore-mentioned emphasizes the need for new and diverse sampling strategies and analytical methods, both spatial and temporal, as well as a balanced interpretation, to cover the existing information gaps.

Being the ground stock of the food chains, primary production must be assessed precisely from both the ecological and economic (e.g. fisheries) standpoints, not only because of the knowledge *per se* but also for the management and preservation of aquatic environments.

2. Measurement of primary production

Determination of phytoplanktonic primary production in tropical coastal lagoons has become controversial, with some ecological principles based on data from temperate latitudes (Russell-Hunter, 1970; Odum, 1972; Margalef, 1974; Goldman, 1974; Vollenweider, 1974). Numerous authors have dealt with the measurement and expression of primary production since the classical works of Rhyther in the 1950s. One of the greatest challenges has been to establish a worldwide reliable and compatible methodology. For the study of phytoplanktonic photosynthesis there are essentially four methods for micro- and macro-vegetation with some variations, based on:

1. Production of oxygen in clear and dark bottles (Gaarder and Gran, 1927). The methodological problem with the dark bottle due to excessive light has been solved by using a photosynthetic inhibitor (DCMU) (Legendre et al., 1983). This determination includes also the diurnal oxygen curve of Odum (1956) based on the production of oxygen or its consumption by morning photosynthesis or nocturnal respiration and their equilibrium in open or *in situ* environments. This evaluation is performed by sampling the water every two or three hours to determine dissolved oxygen in a 24-hour period (Leith, 1975; Whittaker, 1975).
2. Incorporation rate of C¹⁴ radioactive carbon (Steeman Nielsen, 1952). An under-estimation implicit in the C¹⁴ methodology is caused by the excretion products that are usually not assessed and which can represent from 0 to 99% of the production, according to the stress caused by the environmental conditions on the organisms (de la Lanza-Espino and Lozano, 1999).
3. Rate of assimilated CO₂ evaluated by alkalinity and pH changes (Beyers and Odum, 1960).

4. Rate of increases in particulate matter per time (Rhyther and Menzel, 1965).

Determination of chlorophyll “a” associated to appropriate light, although not implying time, is an inexpensive index of the productivity of an environment. A range of 0.9 to 3.0 mg C/mg of chlorophyll “a”, is considered a typical value; this quotient varies daily, with a maximum in the morning, a decrease at noon, and a minimum at night (Goldman et al., 1963; Mc Allister, 1963). However, Hall and Moll (1975), among other authors, consider that its determination only enables speculation about photosynthesis, and that it results not only from spatial and temporal variations but also depends on the efficiency of the pigment, since it could be inactive and not proportional to the size and age of the cells. It has been stated that results with chlorophyll “a” are not better than equations used to predict photosynthesis. However, the other techniques, except for the daily oxygen curve, also have disadvantages as a result of isolating the organisms from their natural environment.

Most phytoplankton cells have other pigments, in addition to chlorophyll “a”; these are known as accessories and they serve as energy transporters (Golterman, 1975), protecting chlorophyll “a” from light (Salisbury and Ross, 1969). The ratio of chlorophyll “a” to carotenoids depends basically on the physiological conditions of the cell (Yentsch, 1965). Margalef (1981) relates primary productivity with the structure of the community through pigment proportions to obtain an index of Species Diversity (D_{430}/D_{665}), which not only reflects changes in the composition of the species in the community but also, the physiological state of the population.

From a technical point of view, the concept of Productivity Index (PI) was introduced in the 1960s. This index considers growth kinetics of unicellular organisms (marine phytoplankton), which has been poorly appreciated (Strickland, 1966). This is mainly due to the fact that the primary net production of the phytoplankton provides little information on the intensity of the production or vitality of a population: large biomasses can photosynthesize with lower rates and small biomasses can have high production rates. Therefore a better understanding of biomass diversity and net production of endemic populations is necessary. Hence, in order to be precise, evolution of the net photosynthetic rate per biomass unit at an optimal light level has to be known (0.1 to 0.15 Langley/min). Therefore, PI is expressed as:

$$PI = \frac{\text{Production rate per biomass (at one unit of light intensity)}}{\text{Amount of biomass}}$$

$$= \frac{dp}{dt} \times 1 = K \text{ at one unit of light intensity}$$

where:

p = biomass

t = time

K = constant

This allows comparing PI values at relevant luminic intensities and the amount of carbon associated with the cells. It must be emphasized that evaluations must be made according to the time of division and growth of the organisms.

Unfortunately, each of these methods yields different results, including measurement units ($\text{gC}/\text{m}^2/\text{h}$, $\text{gC}/\text{m}^2/\text{d}$, $\text{gC}/\text{m}^2/\text{year}$, or the same but using m^3), hindering comparisons (Hall and Moll, 1975; Peterson, 1980; de la Lanza-Espino et al., 1991). The first two methods are the most currently used to measure photosynthesis, and although the bottle method has been valued, some experiments comparing C^{14} and oxygen evolution methods have provided similar results (Williams et al., 1979, 1983).

It is possible to state that in estuarine-lagoon systems, the photosynthetic process in the water column is complex and highly specific in terms of localization. Variations in the same day and site are extreme, which shed doubts on any type of generalization even for the same area (Contreras, 1995). In contrast, the chlorophyll “a” content has been proven to be more constant in any situation, making it a more reliable factor. The relation between chlorophyll “a” and primary productivity, for some authors the "Assimilation Index" (Beerman and Pollinger, 1974), is not reliable, since the response of chlorophyll “a” (i.e., of the phytoplankton biomass), will only be optimal as long as environmental factors are adequate (amount of light, available nutrients and their interrelations), and temperatures are suitable.

3. Temporal and spatial variations

It is evident that changes in environmental conditions (temperature and light) will influence the primary producers, as well as the chemical agents (nutrients) that essentially limit photosynthesis. With regard to environmental conditions, geographic location (particularly latitude), light, depth, time of day, and turbidity (as well as its seasonal variation), are factors to be considered. Availability of nutrients is considered critical in primary production at the oceanic level as it requires rupture of the thermocline, but not in coastal lagoon and estuarine systems, since the river and sediment supplies far exceed the required consumption of nitrogen (nitrates, nitrites, and ammonium) and phosphate (orthophosphates) compounds (in the ratio $\text{C}_{106}, \text{N}_{16}, \text{P}_1$). In temperate latitudes with well-differentiated seasons, there are spring maxima in primary production with nutrient decreases; summer decreases with increased organic matter (rem mineralization), a second maximum of lesser magnitude in the fall, and a maximal remineralization with high availability of nutrients in the winter.

This seasonal pattern is not observed in tropical latitudes, with rainy, dry, and intermediate seasons. “Nortes” or tropical perturbations that mask the four described seasons influence intermediate seasons, and therefore the productive behavior present in temperate climates is not observed. In contrast, spatial variations are more relevant as will be seen in the case studies.

Nixon (1982) proposes a primary production in coastal lagoons ranging from 200 to 400 $\text{gC}/\text{m}^2/\text{year}$, similar to the productions of estuaries and oceanic coastal upwellings (Contreras et al., 1996). However, lower or higher levels can be found resulting from

the local distribution of the photosynthesizers, including regional climate and hydrological features.

Whittaker (1975) proposes the following average of primary productivity referred as dry weight/m²/year for:

Open sea	125 g/m ² /year
Lakes	250 g/m ² /year
Coastal seas	360 g/m ² /year
Algal beds)	
Reefs)	
Estuaries)	1800-2000 g/m ² /year
Swamps)	
Marshes)	

Barnes (1980) considers that although there are many types of coastal-lagoon vegetation, no reason exists to assume that their productivity might differ markedly, and it could increase to 1000 to 4000 g dry wt/m²/year for marshes and mangrove-swamps.

4. Physical setting and primary producers

According to salinity, coastal ecosystems are divided in four large groups:

- Oligohaline (<0.5 to 5.0 psu) dominated by fresh water runoffs, such as swamps, morasses and certain types of marshes and estuaries, mainly located in regions associated with large water flows.
- Mesohaline (5.0 to 18.0 psu) and polyhaline (18.0 to 30.0 psu), such as coastal lagoons resulting from the mixture of rivers and sea waters.
- Eurihaline (30.0 a 40.0 psu) dominated mainly by marine waters, such as bays, coves, and inlets. Their highest incidence is found in areas with scarce or no freshwater runoff and/or arid climates, as for example along Baja California and Yucatan peninsulas, Sonora and parts of Oaxaca, México.
- Hyperhaline (>40.0 psu) such as evaporative lagoons in arid regions.

Coastal lagoons have been classified according to their geomorphological and hydrological characteristics as: isolated, restricted, and open (Kjerfve, 1986), in terms of the number and characteristics of their circulation channels and tidal exchange.

All types of autotrophic organisms proliferate in lagoons and, according to the dominance of one or another, the lagoons are of three types. There are the systems based on phytoplankton, with some seasonal contributions of micro and/or macrophytobenthic organisms in shallow zones, with or without anaerobic autotrophic bacteria, which depend on the stratification of the water column and on the anoxia of the stagnant water on the bottom. Intermediate systems are those based on macroalgae and/or benthic macrophytes. Finally, there are systems based on algal mats in hypersaline lagoons, with intertidal zones subject to prolonged exposures during the dry season.

Comparing activity of all primary producers, i.e. all photosynthesizers, reveals that by volume the phytoplankton is the most important, followed by mangroves and seagrasses. This is because of their restricted production area, despite their high productivity (especially seagrasses).

Despite the diverse scientific works regarding the inter-relation between physical factors and primary production, no statistically significant correlation has yet been established. Some authors searched for a relation between primary production with size, area, lagoon volume/area, and tidal exchanges (in four estuaries and five isolated lagoons), but variability in lagoon behavior is such that none of these inter-relations are relevant. This has been corroborated by Contreras et al. (1996) through correlation of these characteristics in several coastal lagoons in Mexico.

In contrast, other authors found a close association between primary productivity and the reflux rate in five Mediterranean lagoons, and between trophic state and tidal flow in six Brazilian lagoons. All these lagoons were of the isolated type and similar in their morphometry and hydrodynamics, in addition to the fact that their production is based on phytoplankton. Some authors suggest that the distribution and dominance of macrophytes and macroalgae are related to the degree of confinement and to the tidal flow. Isolated lagoons with low water inputs were dominated by the macrophytes *Potamogeton sp.* and *Ruppia sp.* and filamentous green algae, whereas *Zostera sp.*, associated with green and red epiphytic algae, dominated in the lagoons with high water inputs. In these cases, salinity is the main selection factor and is very closely related to tidal exchange.

With shorter time of water residence, primary production in systems based on phytoplankton tends to diminish, whereas systems based on macrophytes tend towards higher production and show an increase in relation to depth, in those without light limitations.

Regarding macro-vegetation, some research points to the dominance of macroalgae in lagoons ranging from shallow, isolated, and enclosed, to restricted ones with substantial supply of anthropogenic nutrients (e.g. Venice, Italy; Nichupté-Bojórquez, Mexico; Piratininga, Brazil, and Peel-Harvey, Australia). Cyanobacterial mats prevail in hyperhaline lagoons and in those characterized by large intertidal zones exposed for a longer time, such as Shark Bay and Spencer Gulf in Australia, Guerrero Negro, and Ojo de Liebre in Mexico, and Long Island Sound in USA.

In many subtropical closed lagoons, marked seasonal changes (dry and rainy seasons), and also to the opening and closing of river mouths, resulting from changes in river flows, are predominant and regulatory factors of both the levels of primary production and the succession of autotrophic organisms (e.g. the coastal lagoons of the Mexican Pacific and of West Australia).

Conditions can be so variable as to originate characteristics that go from mesohaline to hyperhaline, from mesotrophic to hypereutrophic (regarding nutrients) and/or limited by light and nutrients. River flows, depending on their time scale or impact, can either

stimulate photosynthesis through provision of nutrients or suppress it through light limitation as a result of increases in turbidity.

In those ecosystems with multiple confined lagoons and only one communication with the sea, spatial variability can be very high. The geomorphologic configuration of the basins, the depth of their intercommunicating channels and the different depths of each of the components can all have great influence. Accordingly, there can be great differences in salinity, time of water residence, structure of the water column (homogeneous or stratified), limitations of light and nutrients, level of production, and composition of species and populations.

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Biographical Sketches

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