Comparison of calculation procedures of primary productivity by aquatic macrophytes in a shallow tropical coastal lagoon.

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ABSTRACT: Comparison of calculation procedures of primary productivity by aquatic macrophytes in a shallow tropical coastal lagoon. This research aimed to compare some of the most used harvested and demographic methods to estimate net primary productivity (NPP) of aquatic macrophytes, with a recently new proposed method. Samplings were carried out biweekly from June/1997 to June/1998 in the littoral zone of Cabiúnas coastal lagoon (22° and 22° 30' S and 41° 30' and 42° W) located on the north coast of the State of Rio de Janeiro. All stems of an emergent aquatic macrophyte Eleocharis interstincta, were marked with numbered plastic labels in three study plots (0.0625 m²) and their heights measured. The marked stems at each visit were defined as a cohort that was followed until the death of all stems. Biomass samples harvested with a quadrat from the same area (0.0625 m²) were also obtained at each visit. Regression equations were used to relate biomass with the length of the stems. A modified method of Summed Shoot Maximum method was developed for plants with clonal growth and, it takes account the biomass lost by density dependent factors. Of all the harvested methods evaluated in this research, the method proposed by Symbula & Day (1988) was the most appropriate since that it underestimates the net annual primary productivity (NAPP) by only 3.6%. However, it demands efforts of calculating the detritus decomposition rate. Demographic methods like the Allen's Curve and Summed Shoot Maximum had the best performance in estimating NAPP of E. interstincta in tropical environments. The Allen's Curve was more useful to estimate NPP due its accuracy and, being less sensitive to density dependent effects, although it underestimated NAPP by 18.9%.
Key-words: aquatic macrophytes; coastal lagoons; Eleocharis interstincta; methods; primary production.

RESUMO: Comparação dos procedimentos de cálculo de produtividade primária pelas macrófitas aquáticas em uma lagoa costeira tropical. O objetivo desta pesquisa foi comparar alguns métodos mais utilizados, tanto destrutivos quanto demográficos em estimar a produtividade primária líquida (PPL) de macrófitas aquáticas, com um método recentemente proposto. As coletas foram realizadas quinzenalmente de junho/97 a junho/98 na região litorânea da lagoa costeira de Cabiúnas (22° e 22° 30' S e 41°30' e 42° W) localizada no litoral norte do Estado do Rio de Janeiro. Todos os caules da macrófita aquática emergente Eleocharis interstincta foram marcados com etiquetas plásticas numeradas em 3 quadrados de 0,0625 m² e o comprimento de cada caule mensurado. Os caules marcados a cada visita foram definidos como sendo uma "coorte", que foi acompanhada até a morte de todos os caules. Amostras de biomassa coletadas com quadrados da mesma área (0,0625 m²) também foram obtidas a cada visita. Equações de regressão linear foram usadas para relacionar biomassa com o comprimento dos caules. Assim, foi possível estimar o incremento de biomassa das coortes nos quadrados permanentes. Um método modificado do método Somatório dos Caules Máximos, foi desenvolvido para plantas com crescimento clonal e, leva em consideração perdas por fatores dependentes de densidade. De todos os métodos destrutivos avaliados, o método de Symbula & Day (1988) se mostrou mais adequado visto que subestimou a produtividade primária líquida anual (PPLA) em apenas 3,6%.

Porém, demanda esforços para calcular a taxa de decomposição dos detritos. Os métodos demográficos da Curva de Allen e Somatório dos Caules Máximos obtiveram a melhor performance em estimar a PPLA de E. interstincta em ambientes tropicais. A Curva de Allen é preferível em estimar a PPL devido sua maior precisão e, por ser menos sensível a efeitos dependentes da densidade, apesar de ter subestimado a PPLA em 18,9% .

Palavras-chave: macrófitas aquáticas; lagoas costeiras; Eleocharis interstincta; métodos; produtividade primária.

Introduction

The net primary productivity (NPP) is frequently used as a measure of the potential growth of a plant species and its contribution to the ecosystem (Linthurst & Reimold, 1978). Several methods have been devised for estimating primary productivity in aquatic macrophytes, adjusted to different habitats (Smalley, 1959; Wiegert & Evans, 1964; Milner & Hughes, 1968; Mathews & Westlake, 1969; Valiela et al., 1975; Dickerman et al., 1986; Symbula & Day, 1988).

Many harvest methods underestimate NPP because they do not take account of the disappearance of dead material among successive samples (Linthurst & Reimold, 1978). Since that in methods for calculating production from changes in biomass, the correction terms are different and depend upon different assumptions, production estimates for same sites, using different techniques, can be quite disparate. (Kirby & Gosselink, 1976; Linthurst & Reimold, 1978; Dickerman et al., 1986).

Another problem frequently observed is that NPP in higher plants, measured by changes in biomass, is valid only for populations of individuals that all die at the same time. In some communities, shoots may die throughout the growing season while new shoots emerge (Mathews & Westlake, 1969).

In tropical environments, plant populations rarely show a marked growing season. Growth, production and distribution of emergent aquatic macrophytes in tropical environments are influenced, for example, by water level fluctuations (Junk & Piedade, 1993a and b; Furtado, 1994; Palma-Silva et al., 2000; Villar et al., 1996; Santos & Esteves, 2004). During the entire year, production and disappearance (mortality and decomposition) of biomass occur. Thus, traditional methods of estimating NPP in temperate environments can be quite disparate when applied to tropical environments.

Santos & Esteves (2002) developed a new demographic method of estimating NPP, designed for plants with clonal growth that take into account the influence of density dependent factors. This research aimed to compare this new method with some of the most used demographic and harvested methods to estimate of NPP in Eleocharis interstincta (VAHL) Roemer & Schults, an emergent aquatic macrophyte in a tropical coastal lagoon

Study area

The Cabiúnas coastal lagoon has an area of 0,35 km², with a high shoreline index and maximum depth of 3.50 m. It is located on the north coast of Rio de Janeiro State, between the municipal districts of Macaé and Carapebús (22º and 22º 30' S and 41º30' and 42º W). Its origin is associated with the appearance of sandbars during the last marine regression (Esteves, 1998). The sandbar between the lagoon and the ocean is sometimes opened, in order to control the effect of the floods and/or to allow the entrance of commercial fish species (Faria et al., 1994; Albertoni et al., 1999). A sub-humid/humid climate with no or little deficit of water is typical for the region. The mean annual relative humidity is 83% and the mean annual temperature around 22 ºC. Mean summer temperature (January) and the mean winter (July) are 25 ºC and 19 ºC respectively. The annual average rainfall (1,300 mm) are concentrated in spring and summer (from September to February)

with drought during winter. The winds blow the whole year with prevalence from the Northeast, and to a smaller degree East, Southeast and Southwest (Fiderj, 1977).

Some littoral areas of Cabiúnas lagoon have dense stands of Typha domingensis and Eleocharis interstincta. In the deepest zone, Nymphaea ampla and Nymphoides humboldtiana predominate (Henriques et al., 1988).

Material and methods

Samplings were carried out biweekly from June, 1997 to June, 1998 in one of the embayment of the lagoon. In the littoral zone, three 0.0625 m² study plots were positioned in the center of the E. interstincta stand, in parallel to the shoreline. In each plot, all stems were tagged with numbered plastic labels and the height of each stem (measured from the sediment-water interface to the apical portion of the stem) was measured. In each examination every newly emerged stem in the study plots was also tagged, constituting a new cohort which was followed until the death of all stems. The water level was measured in the same point of the study plots.

Three quadrats of 0.0625 m² were harvested (including belowground biomass) in the same area of the study plots. The material obtained in those quadracts was used to determine NPP using the methods described below. In the laboratory, the samples were washed with running water and separated in stems (more than 50% of the length constituted of chlorophyllous tissue) and detritus (less than 50% of the length constituted of chlorophyllous tissue).

The stems were measured, dried in an oven to constant weight to obtain their individual biomass. Regression equations between the biomass and the stem height (log transformed data) for each sample date were obtained.

Calculation of the net primary production (NPP)

The NPP of E. interstincta was calculated with the cohort data and it is a modification of the Summed Shoot Maximum method described by Dickerman (1986). In each cohort, maximum biomass registered for each stem was followed, independent of the time (life time) that this maximum biomass was reached. The stem with maximum individual biomass was chose as "maximum potential biomass", which was then multiplied by the initial density of the cohort. This procedure allowed the estimation of the maximum potential biomass incorporation for each cohort, since all the stems of the cohort would have, potentially, the same incorporation capacity.

$$NPP = n.B_{máx}$$

where: n is the initial stem density and $B_{máx}$ is the maximum stem biomass of the respective cohort.

Using this method, it is assumed that difference does not exist in the stems genotype, i. e., individuals would be clones (ramets). Thus, factors that could regulate the biomass incorporation for each stem (competition, mortality and herbivory), during its lifetime, would be eliminated. In order to calculate net annual primary productivity (NAPP), NPP of each cohort was summed (Santos & Esteves, 2002). Since this method requires labor work and estimates NPP at individual basis, it was used as a "standard" against the other methods described below were compared.

The **Summed Shoot Maximum method** (SSM) described by Dickerman (1986). Annual maximum dry mass of every individual shoot in the study plots was calculated using regression equations that correlate shoot height with biomass. The maximum masses of all shoots were summed for each year to estimate NAPP.

The **Allen's Curve method** is able to detect many characteristics of growth and development of populations, particularly phases of apparent negative production and high mortality (Mathews & Westlake, 1969). The cohort production is calculated graphically, relating the mean biomass per shoot with the density of shoots. Cohort production is equal to the total area below the curve (Fig.1).
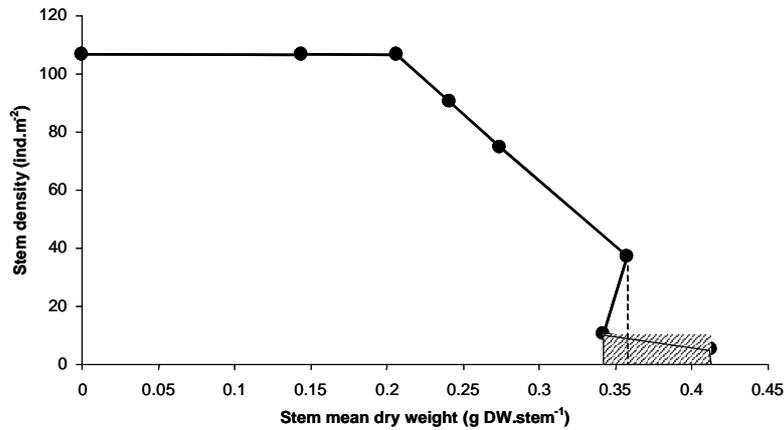
Figure 1: Exemplary Allen Curve used for estimating the NPP of *E. interstincta* in the Cabiúnas coastal lagoon. NPP corresponds to the area bounded at the top by the solid line, on the right by the dashed vertical line and, on the bottom and on the left by the axes of the graph. The shaded area indicates production, which is added to calculate total production of the cohort. NAPP is then calculated by the sum of NPP of each cohort.

The **Wiegert & Evans (1964) method**. Wiegert & Evans (1964) proposed a method to evaluate primary productivity based on alterations in live biomass and the decomposition rate of detritus. Estimates of instantaneous rate of disappearance of dead plant material (= litter) are measured using replicated paired plots. All living plant material in each of two plots sharing a common border is removed by clipping, and the litter in one of the two plots is harvested and weighed. After a known interval of time, the site is revisited and the litter remaining in the other plot is harvested. The instantaneous rate of litter disappearance (r_i) is then:

$$r_i = (\ln(m_0/m_1))/(t_1-t_0)$$

where: m_0 is the mass of litter at t_0, and the rate of litter loss (r_i) is in units of grams per gram per day.

The amount of dead plant material that disappeared (x_i) in any interval (Δt) is computed next using changes in the amount of dead plant material during that interval:

$$x_i = ((a_i + a_{i-1})/2)r_i \, t_i$$

where: a_{i-1} corresponds to the quantity of all dead material at the start of the interval, a_i is the total amount of dead material remaining at the end of the interval t_i.

Changes in living biomass (Δb) and dead standing material (Δa) are then computed as:

$$\Delta b = b_i - b_{i-1} \text{ and } \Delta a = a_i - a_{i-1}$$

Mortality (d_i) is determined using both the amount of disappearing dead plant material and changes in dead standing material:

$$d_i = x_i + \Delta a_i$$

Finally, net production (y_i) is calculated as the sum of living biomass changes and mortality:

$$y_i = \Delta b_i + d_i$$

For calculation of the decomposition rate of E. interstincta, we used the data of Brum (2000), which determined a rate of 4.7 x 10^{-3} g DW day^{-1}.

The **Maximum Biomass method**. One of the methods to evaluate NPP is based on changes in biomass during the growing season. It is particularly useful for communities that show a marked annual fluctuation in biomass and which are subject to few losses (mortality and herbivory) during the growing season. If the initial biomass or losses during the growing season before the maximum standing crop are negligible, determination of maximum biomass is considered sufficient. (Westlake, 1963). No corrections for biomass losses during the growing season are included and NAPP corresponds to the maximum value of biomass during the year.

The **Milner & Hughes (1968) method**. The carryover of biomass from one growing season to the next is considered by summing only positive changes in live biomass for all sampling intervals:

$$NAAP = \sum_{i=1}^{n} (\Delta b_i)$$

The **Smalley (1959) method**. In this method, the undetermined fraction of the live vegetation lost between sampling periods is included in the calculation, thus underestimating true net production. However, the calculations didn't include apparently negative production, thus tending to bias sampling errors upward (Kirby & Gosselink, 1976). Positive changes in live biomass between sampling times are considered and corrections for losses during the time interval are also considered by changes in dead standing crop:

NPP = Δb + Δa when Δb › 0 and Δa ›0;
= 0 when Δb ‹ 0 and Δa ‹0;
= Δb when Δb › 0 and Δa ‹0;
= Δb + Δa when Δb ‹ 0 and Δa ›0.

If the live standing crop changes are negative, i.e. (Δb ‹ 0), monthly production is equal to the algebric sum of live and dead standing crop changes (Δb + Δa) or set to zero, whichever is larger.

The **Valiela et al. (1975) method**. It is similar to the Milner and Hughes method and losses of dead material over growing season are summed to estimate NAAP. This method was designed for areas with a negligible litter component, and a steady-state system is assumed in which production rates are balanced by decomposition rates. The amount of living plant biomass (e) that dies but is not included as dead standing material is calculated as:

e = - Δa when Δb › 0 and Δa ‹0;
e = - (Δb +Δa) when Δb ‹ 0

The variables a and b are defined as in the Wiegert and Evans method described above. If only live plant biomass contributes to the standing dead component, (e) it cannot be negative. If a negative (e) occurs for any interval, it is set to zero.

The **Symbula & Day (1988) method**. This method, originally delineated to estimate belowground production (root production), is exactly equal to Wiegert & Evans (1964) method, with a slight modification: if $a_i - a_{i-1}$ ‹ 0 then the decomposition term becomes $a_{i-1} - a_i$. When dead material is declining, the amount decomposed would be underestimated by applying the decay rate to the average dead material for the sample interval (Symbula & Day, 1988). If there are no additions to the dead material pool, the decomposed amount equals $a_{i-1} - a_i$. Mortality must be zero (Wiegert & Evans, 1964). If NPP for a given sample interval was negative, it was assumed to be zero because negative values should not be possible with this method since mortality is taken into account. High data variability and/ or underestimates of mortality can cause negative values (Symbula & Day, 1988).

The accuracy of each method to estimate NAPP was compared by relative deviation (RD) that is given by the formula:

$$RD = \acute{a} \mid p\text{-}P \mid$$

where: p is the partial (monthly or whatever was the sampling interval) NPP of a given method and P is the partial NPP of Santos & Esteves method.

Results

The relationship between dry weight and stem height was significantly different among sampling intervals (Santos, 1999). Thus, discrete equations were used in each sampling interval in order to estimate the stem weight increment in the study plots.

During the study period, no growth originating from sexual reproduction (seed germination) was observed. In the harvested below ground biomass, all rhizomes were connected by stoloms, which characterizes only vegetative reproduction. NAPP estimates for E. interstincta (calculated with the different methods) are shown in Tab. I.

The data obtained by Maximum Biomass method does not make corrections for biomass losses during the growing season, and for that reason the discrepancy in the NAPP estimates was the largest.

Table I: Comparison of NAPP estimates for E. interstincta calculated by harvested and demographic methods with the data computed by Santos & Esteves (2002) method. The (-) sign represents the underestimated percentage and (+) the overestimated percentage in relation to estimates of Santos & Esteves (2002).

Methods	References	NAPP (gDWm⁻²year⁻¹)	Difference %
	Santos & Esteves (2002)	1,012.87	-
Harvested methods	Maximum biomass (Westlake, 1963)	338.84	(-) 66.55
	Milner & Hughes (1968)	422.38	(-) 58.30
	Smalley (1959)	619.32	(-) 38.86
	Valiela at al. (1975)	1,155.98	(+) 14.13
	Wiegert & Evans (1964)	805.65	(-) 20.46
	Symbula & Day (1988)	976.43	(-) 3.60
	Maximum biomass (Westlake, 1963)	338.84	(-) 66.55
Demographic methods	Allen's Curve (Mathews & Westlake, 1969)	821.35	(-) 18.91
	SSM (Dickerman, 1986)	739.90	(-) 26.95
	Allen's Curve*	734.19	(-) 27.51
	SSM*	671.74	(-) 33.68

* Calculations done with only one regression equation integrating all sampling intervals.

The NAPP calculated through the Milner and Hughes method produced an underestimation of 58.3%, because only positive changes in live biomass are considered. This discrepancy is still maximized by the fact that the detritus dynamics are also not considered, and had a considerable importance in tropical environments.

Through the Smalley method, although corrections for changes in dead material are included, an underestimate of NAPP was found since one of its assumptions is to consider it null when negative values of NPP occurs, either for live biomass as for dead material. The primary productivity of E. interstincta is related with the water level (Santos, 1999) and the decrease in live biomass, when the habitat is receding due winter downdraught is systematic. Thus, negative values for changes in live biomass were obtained. This method was not accurate to evaluate seasonal variations in NPP of this aquatic macrophyte in Cabiúnas lagoon.

The only method in that it was observed an overestimation of NAPP is Valiela et al. (1975) procedure. It was due to the losses correction of live biomass by mortality and losses by changes in dead component (e) and overestimates of these values are produced when live biomass variation and changes in dead material along the sampling interval show negative values.

Using the Wiegert & Evans (1964) method, although corrections for the decomposition rate are included, an underestimation of NAPP was found. Besides this method computes positive changes for live biomass, the term (d_i) that corrects for mortality losses, has to be larger or equal to zero (Wiegert & Evans, 1964). As $d_i = x_i + Da_i$, only positive changes in dead components are computed. Thus, situations of negative changes (apparent negative production) are set to zero leading an underestimation of NAPP.

In the Symbula & Day (1988) method, the modification done in the term Da_i of the original Wiegert & Evans (1964) method works quite well. This modification computes situations in which negative values occurs for the dead components and seasonal variations in NPP seems not affect NAAP estimates underestimating it by just 3.6%.

The Allen's Curve technique was the demographic method that showed smaller discrepancy in estimating NAPP, underestimating it by 19%. When only one regression equation integrating all the sampling periods was applied, an increase in sampling bias error was observed (27.5%). Although this method was the most accurate, it showed an increase in bias error when stem density increase (Fig. 2a).

The demographic method of Dickerman (1986) also showed bias error by density dependent effects, which can influence estimates of NAPP. This bias estimate error can be intensified in populations and/or periods with high density (Fig. 2b). Like Allen's Curve, an increase in sampling bias error was also observed when only one regression equation was used (Tab. I)
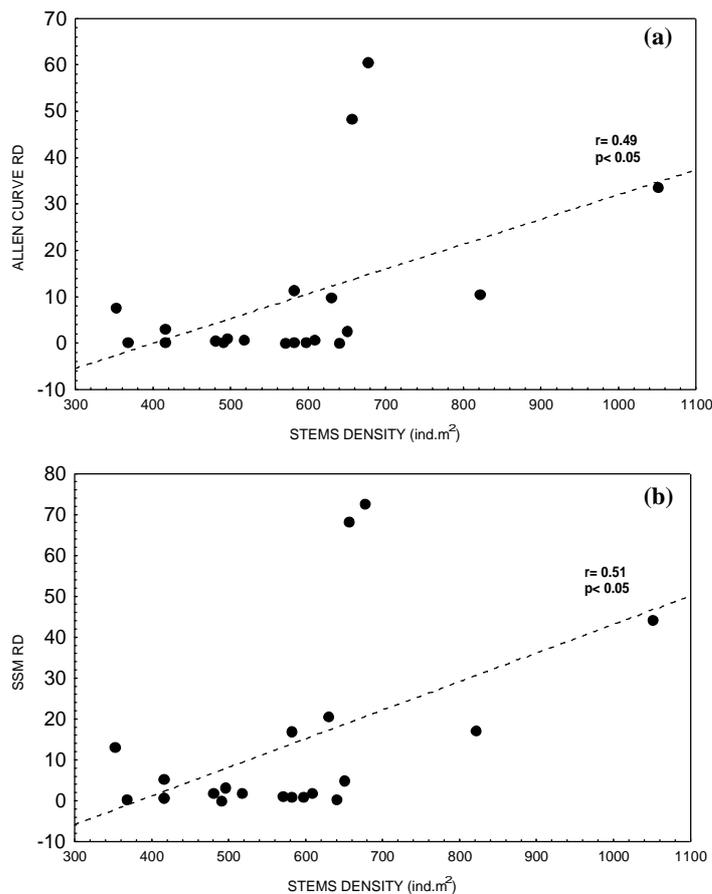

Figure 2: Correlation between relative deviation (RD) of Allen curve (a) and SSM (b) methods with stem density of *E. interstincta* during sampling periods.

Table II: Relative deviation (RD) of NAPP estimates in relation to Santos & Esteves (2002) method.

Methods	References	RD
	Milner & Hughes (1968)	661.0
	Smalley (1959)	597.8
Harvested	Valiela at al. (1975)	807.7
methods	Wiegert & Evans (1964)	523.0
	Symbula & Day (1988)	465.2
Demographic	Allen's Curve (Mathews & Westlake, 1969)	191.5
methods	SSM (Dickerman, 1986)	275.2

Discussion

Most methods used to estimate primary productivity were conceived in temperate environments. Methodological problems are mitigated when there exists a well defined growing season which begins in spring and continues in to late fall - early winter. In this period, the temperature and/or solar radiation causes mass mortality of vegetation, except for rare cases.

As most in these methods, it is assumed that the growth of plants occurs in a single and continuous period, i. e., an increase and cumulative process of live biomass occurs. Any variation in this pattern, as for example mortality during the growing season (negative live biomass production), can lead to bias in NAPP estimates. Thus, the use of some simple methods, such as Maximum Biomass, cannot supply a reasonable estimate of NAPP. But, these methods do not have the same accuracy in tropical environments. The absence of a well-defined growing season in the tropics, and the occurrence of a continuous recruitment of new individuals/shoots during the entire year result in more complex production dynamics and decomposition processes of plant biomass.

The Maximum Biomass method is frequently used to estimate annual net primary productivity in temperate environments, but production is always underestimated when compared with data from other methods in the same environment (Kirby & Gosselink, 1976; Dickerman et al., 1986; Wetzel & Pickard, 1996). Maximum standing crop for Phragmites communis underestimated productivity by 14.6% when compared with Allen's Curve, while for Typha angustifolia, the underestimate was 28% (Mason & Bryant, 1975). The error in using peak standing crop as an estimate of net productivity is serious, especially when detailed energy and nutrient budgets for an entire environment are computed (Mason & Bryant, 1975).

In order to use the demographic methods to estimate net primary productivity, a regression equation that correlates the biomass increment to length or plant area is necessary. A considerable source of errors in this relationship can occur since a seasonal variation or a variation according to different size classes within a population can sometimes be observed (Hopkinson et al., 1980). When only one regression equation was used for NAPP calculations by Allen's Curve and SSM method, underestimates of NAPP were found when compared with height-mass regression equations obtained at each sample period. The apparent stability of tropical environments leads to a generalization about the ecological processes (production, decomposition) and can induce methodological error when the particularities of each environment are not considered.

Seemingly, the most adequate NAPP estimates of E. interstinca in this research was produced using the Symbula & Day method (Tab. I). But, when the NPP values among the samplings periods (partial estimations) are observed, the Symbula & Day method was not so adequate, showing low accuracy in detecting intrinsic NPP fluctuations when compared with data from the Santos & Esteves method (2002). This low accuracy can be exemplified by the relative deviation (RD) of Symbula & Day method (Tab. II).

RD shows the dispersion of each method in the NPP estimates. Even using the Symbula & Day method, which had the smallest discrepancy in NAPP estimates, its relative

deviation was not one of the smallest, indicating a great variability in the partial estimates during the sampling period. The value obtained by the demographic method of Allen's Curve presented the smallest dispersion in the NAPP estimates, being the most sensitive method in detecting the intrinsic variations in NPP of this population.

Neither the SSM nor the Allen's Curve methods were appropriate in detecting density dependent differences in NPP (Fig. 2). An increase in bias error was observed in the estimates of NPP by both methods when the population of E. interstincta exhibited higher densities (p ‹0.05).

Ecologists interested in the dynamics of communities, rather than their description, are deeply concerned with the magnitude of the primary photosynthetic production and the factors influencing it because the rate of primary production is ultimately one of the main factors controlling the rates of multiplication and growth of the organisms in a community (Westlake, 1963). Thus, an accurate estimate of primary productivity of a given population depends as much on the intrinsic characteristics of the ecosystem as the methods used in the estimation.

Because of the dynamics of tropical environments, the use of methods that do not make corrections for biomass losses due to mortality during sampling intervals, can greatly underestimate NAPP. Thus, the more useful methods in these environments are those that incorporate corrections for biomass losses during sampling intervals. In demographic methods, cohorts can be used with relative ease, in emergent aquatic macrophyte species and in shallow environments, where water level fluctuation is low. In environments with great water level fluctuation and other kinds of aquatic macrophytes (submerged, free-floating, rooted with floating leaves), the demarcation of new cohorts can be difficult, which makes these methods difficult to use.

Data from demographic methods such as Allen's Curve and SSM had the best performance in estimating NAPP of E. interstincta in Cabiúnas coastal lagoon. Allen's Curve method was more useful to estimate NPP due its accuracy and being less sensitive to density dependent effects. The SSM method was shown less efficient in detecting density dependent variations in NPP. This better performance of the demographic methods implies an increase of labor in the field and in the laboratory, since these methods require cohort tracking. Possible sources of error in the use of demographic methods are the regression equations used to determine the increment of individual biomass by length or plant area measures. It is advisable that discrete equations obtained at each sampling interval be used since the biometric relationships can show seasonal variations. In this research, both demographic methods underestimated NAPP when only one equation that integrated all the sampling periods was used.

Of all the harvest methods evaluated in this research, Symbula & Day method was shown the most appropriate to estimate the NAPP. Besides incorporating biomass losses due mortality and applying a decay rate to average dead material, it corrects situations where there are negative values for changes in live biomass during sampling periods. These situations of apparent "negative" production are frequently found in tropical environments. Another advantage of this method is that it can also be used for any environment or kind of aquatic macrophyte.

Aknowledgments

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