An economical non-destructive method for estimating eelgrass, *Zostera marina* (Potamogetonaceae) leaf growth rates: formal development and use in northwestern Baja California

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Abstract: Seagrass beds provide much of the primary production in estuaries; host many fishes and fish larvae, and abate erosion. The present study presents original analytical methods for estimating mean leaf-growth rates of eelgrass (*Zostera marina*). The method was calibrated by using data collected in a *Z. marina* meadow at Punta Banda estuary in Baja California, Mexico. The analytical assessments were based on measurements of leaf length and standard regression procedures. We present a detailed explanation of the formal procedures involved in the derivation of these analytical methods. The measured daily leaf-growth rate was 10.9 mm d^{-1} $leaf^{-1}$. The corresponding value projected by our method was 10.2 mm d^{-1} $leaf^{-1}$. The associated standard errors were of 0.53 and 0.56 mm d^{-1} $leaf^{-1}$ respectively. The method was validated by projecting leaf-growth rates from an independent data set, which gave consistent results. The use of the method to obtain the mean leaf growth rate of a transplanted plot is also illustrated. Comparison of our leaf-growth data with previously reported assessments show the significant forcing of sea-surface temperature on eelgrass leaf dynamics. The formal constructs provided here are of general scope and can be applied to equivalent eelgrass data sets in a straightforward manner. Rev. Biol. Trop. 56 (3): 1003-1013. Epub 2008 September 30.

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Seagrass beds are indicators of the status of the coastal zone and can be used in management strategies that aim to preserve or improve environmental quality. Nutrient cycling represents a large proportion of the environmental services performed by estuaries and seagrass beds (Wharton 1970, Gosselink *et al*. 1974, Costanza *et al*. 1997). In particular, eelgrass populations provide substantial amounts of organic material to the shallow-water food web, as well as habitat or shelter for many fishes and fish larvae (McRoy 1966).

Sea-surface temperature exerts a strong influence on the dynamics of marine ecosystems (Tegner and Dayton 1987, Baumgartner *et al*. 1992, Beer and Koch 1996, Holbrook *et al*. 1997, Johnson *et al*. 2003). For eelgrass, water temperature drives the accumulation of above-ground biomass (Poumian-Tapia and Ibarra-Obando 1999), and is highly correlated with leaf dynamics (Solana-Arellano *et al*. 1997, Short and Neckles 1999, Solana-Arellano *et al*. 2004). Sea-surface temperature has been reported to control the seasonal cycle of eelgrass growth (Rasmmussen 1977, Phillips and Backman 1983). There is also a widespread belief that both the distribution and abundance of seagrasses in temperate littoral waters are tightly linked to light availability (Backman and Barilotti 1976, Dennison and Alberte 1982, 1985, 1986, Bulthuis and Woelkerling 1983, Orth and Moore 1983, 1988, Zimmerman *et al*.

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 56 (3): 1003-1013, September 2008

1003

1991, Cabello-Pasini *et al.* 2002). Data collected at our study site in Punta Banda corroborate that sea surface temperature, light availability and dissolved nutrients are key environmental factors that control leaf dynamics in eelgrass (Solana-Arellano *et al*. 2004). A principal-component analysis resulted in a highest correlation coefficient for sea-surface temperature (r=0.86), while light radiation also had a high correlation coefficient (r=0.72). Together these two variables explain 49 % of the variability induced by all abiotic variables.

Changes in the global climate are expected to alter sea-surface temperature, underwater light flux, and the availability of dissolved nutrients, and thus may severely affect both the structure and the dynamics of seagrass beds (Cambridge and McComb 1984, Valiela *et al*. 1992, Peterson *et al*. 1993, Short and Neckles 1999). In addition to adverse climatic influences, coastal development represents an additional threat to the health and extent of seagrass beds that could result in irreversible alterations. The ecological importance of seagrasses has driven efforts to conserve and expand existing communities, restore lost ones and create new ones. Indeed, several workers have developed various techniques for transplanting seagrass species (Fredette *et al*. 1985, Fonseca *et al*. 1986, Lewis 1987, Fonseca *et al*. 1996).

The disruptive effects of coastal development are evident in many estuaries and salt marshes throughout adjacent southern California, USA (Fong and Zedler 2000, Linding-Cisneros and Zedler 2000, Werner and Zedler 2002). Human activities in Baja California (Mexico) wetlands and estuaries have accelerated in the last decades. The first structural modification of an estuary on the Pacific coast of the peninsula was the 1983 construction of an oil-industry tidal exclusion in the Punta Banda estuary, which resulted in the disappearance of vegetation within the affected area. Prior to 1979, the site was practically undisturbed and had extensive coverage of eelgrass (Aguilar-Rosas 1980). Eelgrass populations within the remaining tidal zone were considered depleted by 1983 (Cabello-Pasini

1984) because of burial provoked by heavy storms that occurred during 1978-1981. Transplantation of *Z. marina* shoots from a nearby estuary has been contemplated as a way to promote the recovery of the depleted *Z. marina* beds at our study site (Cabello-Pasini 1984, Solana-Arellano *et al.* 2002).

Data on structural and dynamical aspects of vegetation in re-established wetlands are required to provide evidence that restoration efforts have met predefined goals. The rate of change for leaf length in *Zostera marina* has been considered as a response variable to environmental influences (Jacobs 1979, Phillips and Backman 1983, Short and McRoy 1984). The leaf architecture of *Z. marina* makes length a determinant of both leaf area and weight (Solana-Arellano *et al.* 2003). Hence the characterization of the corresponding leaf-growth rates provides valuable ecological information.

Studies on leaf dynamics of seagrasses have generally been descriptive (Sand-Jensen 1975, Jacobs 1979, Ott 1980, Aioi *et al.* 1981, Umebayashi 1988, Aioi and Pollard 1993). Methods for the analytical assessment of leaf growth are scarce in the literature. The first analytical study on growth rates for sea grasses was developed by Patriquin (1973), who proposed a linear model for the mean growth rate of previously marked shoots of *Thalassia testudinum*. Solana-Arellano *et al.* (1997) studied the dynamics of leaf growth rates for *Z. marina* through a generalization of the mono-molecular model.

Due to seasonality effects, the study of representative variables of leaf dynamics in *Z. marina* demands extensive sampling during the entire yearly cycle. Traditional methods for the assessment of eelgrass leaf-growth rates require tedious leaf-marking techniques and time-consuming laboratory work. These procedures can induce high shoot loss, particularly in restored areas. In the present study we introduce analytical tools for the estimation of mean leaf-growth rates and their associated uncertainties. The results show that these indirect assessments produce consistent outcomes for both natural

and transplanted eelgrass populations at our study site.

MATERIALS AND METHODS

Study site: the data used to calibrate the analytical method developed in this paper were collected biweekly from January through December 2000 in a *Z. marina* meadow in Punta Banda estuary, located near Ensenada, Baja California, Mexico ($31°40'$ N- $31°48'$ N and $116°37'$ W-$116°40'$ W). A complete description of the study site is given in Solana-Arellano *et al.* (2000).

Field laboratory and statistical methods: following a complete random sample design, we marked 20 shoots during each sampling date, using the technique of Kentula and McIntire (1986). After two weeks, we harvested the previously marked shoots and marked a new set of 20 shoots. The samples were taken to the laboratory where measurements of length (mm), width (mm), and dry weight (g) were made on each leaf. Individual mean leaf-growth rates, expressed as *mm d⁻¹*, were calculated by dividing leaf elongation by the number of days of growth. We collected a total of 600 shoots and 2 263 complete leaves for the analysis. Curve fittings were made by using non-linear regression in the statistical package STATISTICA (1999).

The analytical mean leaf-growth rate projection method: for the constructs presented throughout this work, the following definitions and notations are required. Let $l(t)$ be the length of a *Z. marina* leaf at time t. The number of *Z. marina* leaves contained in a shoot sample taken at time t_i with $t_0 \leq t_i \leq t_F$ will be denoted by $N(t_i)$. For $j = 1, \ldots\ldots N(t_i)$ let $l_j(t_i)$ stand for the length of the jth leaf in the sample. The symbol $\alpha_j(t_i)$ will denote the expected value of $l_j(t_i)$ over the distribution of leaf lengths. The corresponding variances will be denoted by means of $\beta^2_j(t_i)$. Similarly $\Delta(t_i, t_{i+1})$ will stand for the time increment $(t_{i+1} - t_i)$, while the symbol $\Delta l_j(t_i, t_{i+1})$ will denote the leaf length increment $(l_j(t_{i+1}) - l_j(t_i))$. Thus, for the jᵗʰ leaf,

the mean leaf growth rate (MLGR) over the interval (t_i, t_{i+1}) is defined by,

$$\frac{\Delta l_j(t_i, t_{i+1})}{\Delta(t_i, t_{i+1})} = \frac{l_j(t_{i+1}) - l_j(t_i)}{(t_{i+1} - t_i)} \qquad (3.1)$$

The expected value over the associated variation range of these MLGR will be denoted by the symbol $\alpha_{rl}(t_i, t_{i+1})$. Correspondingly, the variance of these MLGR in equation (3.1) will be represented by means of the symbol $\beta^2_{rl}(t_i, t_{i+1})$.

Suppose that a leaf survives the deleterious effects of drag forces or herbivory. Then its growth could take place continuously over a suitable period of time. Therefore, it is reasonable to assume that there exists a longitudinal asymptotic maximum size l_∞, which is the maximum length attained in the limit when time approaches infinity. This is a standard assumption in growth models (Von Vertalanffy 1957, Richards 1959, Seber and Wild 1988), and corresponds to a simplification that can be tested by empirical validation. Solana-Arellano *et al.* (1997) used this framework and demonstrated that leaf dynamics in *Z. marina* could be modeled through a generalization of the traditional monomolecular model. They demonstrated that the associated asymptotic specific-growth rate can be expressed as an environmental forcing function of temperature, underwater light flux, and dissolved nutrients. In this section, we will also invoke the monomolecular growth assumption, and use it to derive an original analytical method for the projection of the pertinent MLGR values. We assume that $l(t)$ can be modeled by means of the equation

$$\frac{dl}{dt} = \phi(t)(l_\infty - l(t)) \qquad (3.2)$$

where $\phi(t)$ stands for an environmental forcing factor. Separation of variables and integration from t_i to t_{i+1} produces the equivalent equation,

$$\ln\left(\frac{l_\infty - l_j(t_{i+1})}{l_\infty - l_j(t_i)}\right) = -\int_{t_i}^{t_{i+1}} \phi(u)du. \qquad (3.3)$$

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 56 (3): 1003-1013, September 2008

1005

Taking exponentials on both sides and rearranging we have,

$$l_j(t_{i+1}) = l_\infty - (l_\infty - l_j(t_i)) \ \exp\left(-\int_{t_i}^{t_{i+1}} \phi(u) du\right)$$

(3.4)

Subtracting $l_j(t_i)$ from both sides of equation (3.4), we get an analytical representation for the individual MLGR in equation (3.1). It becomes,

$$\frac{\Delta l_j(t_i, t_{i+1})}{\Delta(t_i, t_{i+1})} = \frac{(l_\infty - l_j(t_i))}{\Delta(t_i, t_{i+1})}\left(1 - \exp\left(-\int_{t_i}^{t_{i+1}} \phi(u) du\right)\right)$$

(3.5)

Obtaining the expected value on both sides of the above equation will produce analytically determined values for $\alpha_{rl}(t_i, t_{i+1})$, these will be expressed in terms of $\alpha_l(t_i)$, the expected value of leaf length at a time t_i, the asymptotic length l_∞ and the scaling function $\phi(t)$. Formally,

$$\alpha_{rl}(t_i, t_{i+1}) = \frac{(l_\infty - \alpha_l(t_i))}{\Delta(t_i, t_{i+1})}\left(1 - \exp\left(-\int_{t_i}^{t_{i+1}} \phi(u) du\right)\right)$$

(3.6)

By a direct calculation of the variance on both sides of equation (3.5) we get an expression of $\beta^2_{rl}(t_i, t_{i+1})$, which represents the projected variance for the MLGR over the interval $t_i < t < t_{i+1}$. It becomes,

$$\beta^2_{rl}(t_i, t_{i+1}) = \left(\frac{1 - \exp\left(-\int_{t_i}^{t_{i+1}} \phi(u) du\right)}{\Delta(t_i, t_{i+1})}\right)^2 \beta^2_l(t_i)$$

(3.7)

The analytically defined values of equation (3.6) and (3.7) are based on both the $\alpha_l(t_i)$ data and on the values that the scaling factor

$\phi(t)$ attains at each sampling time t_i Directly obtained leaf-length values determine sample values for $\alpha_l(t_i)$. We will propose a method to estimate the factor $\phi(t)$ which can be identified by means of standard regression procedures, using leaf length data. To obtain that device, we observe that if we define a continuous function $r(t)$ through the expression

$$r(t) = \frac{\phi(t)(l_\infty - l(t))}{l(t)}$$

(3.8)

then equation (3.2) can be reparametrized into the form

$$\frac{dl}{dt} = r(t)l(t)$$

(3.9)

Then separation of variables and integration from t_0 to t_{i+1} yields for the jth leaf in a sample

$$l_j(t_{i+1}) = l_{jo}(t_{i+1}) \ \exp\left(\int_{t_i}^{t_{i+1}} r(u) du\right)$$

(3.10)

where $l_{j0}(t_{i+1})$ stands for the length that the jth leaf in the sample taken at time t_{i+1} had at the initial sampling time t_0. Similarly, integration from t_0 to t_i produces,

$$l_j(t_i) = l_{j0}(t_i) \ \exp\left(\int_{t_0}^{t_i} r(u) du\right)$$

(3.11)

Form the above equations, mathematical expectation gives

$$\alpha_l(t_i) = \alpha_{l0}(t_i) \ \exp\left(\int_{t_0}^{t_i} r(u) du\right)$$

(3.12)

and

$$\alpha_l(t_{i+1}) = \alpha_{l0}(t_{i+1}) \ \exp\left(\int_{t_0}^{t_{i+1}} r(u) du\right)$$

(3.13)

1006

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 56 (3): 1003-1013, September 2008

In the above equations $\alpha_{l0}(t_i)$ and $\alpha_{l0}(t_{i+1})$ represent the expected values of the random variables $l_{j0}(t_i)$ and $l_{j0}(t_{i+1})$ respectively. Combining equation (3.12) and (3.13) we get,

$$\alpha_l(t_{i+1}) = \alpha_l(t_i)s(t_i) \quad \exp\left(\int_{t_i}^{t_{i+1}} r(u)du\right)$$

(3.14)

where

$$s(t_i) = \frac{\alpha_{l0}(t_{i+1})}{\alpha_{l0}(t_i)}$$

Following Charles-Edwards *et al.* (1986) and Solana Arellano *et al.* (1997), we can assume that seasonal influences on leaf growth induce a periodic behavior for the functions $s(t)$ and $r(t)$. These functions can be approximated by means of trigonometric polynomials (cf. equation (5.9.10) in Batschelet (1974)). Formally, r(t) and s(t) can be assumed to have the empirical form,

$$r(t) = a_{r0} + \sum_{k=1}^{m} a_{rk}cos(c_r t) + b_{rk}sin(c_r t)$$

(3.15)

$$s(t) = a_{s0} + \sum_{k=1}^{n} a_{sk}cos(c_s t) + b_{sk}sin(c_s t)$$

(3.16)

where c_r and c_s as well as a_{rk}, a_{sk}, b_{rk} and b_{sk} for k=0,1,....m or n are parameters, with m, and n being the orders of the trigonometric polynomials under consideration.

These projection procedures can be summarized in the following steps. We first obtain an estimate for the maximum asymptotic length directly from observations. That is, we assume that l_∞ is represented by the maximum value that $l(t)$ has attained over a long period of observations. Then, we assume that $r(t)$ and $s(t)$ are given by trigonometric polynomials (cf. equations (3.15) and (3.16)), and perform the

fitting of the resulting equation (3.14) by using values for $\alpha_l(t_i)$ determined from samples. This will provide an identified form for $r(t)$ and through the use of equation (3.8) we can obtain an estimate of $ø(t)$. We then use these estimations, along with the values for $\alpha_l(t_i)$ determined from samples to produce, by means of equation (3.6), the corresponding projected average MLGR values. The associated projected variances $\beta^2_{rl}(t_i, t_{i+1})$ are given by the pertinent procedures defined by equation (3.7).

RESULTS

Projected mean leaf growth rate values: for the projection of MLGR we used a maximum leaf length of 863 mm, which was reached after 32 months of observation in November 1998 (Solana-Arellano 2004). This value was used as an estimation for l_∞. To find expressions for both $r(t)$ and $s(t)$ (and assuming they have a trigonometric polynomial representation (cf. eq. (3.15) and (3.16)), we fitted equation (3.14) by using values for $\alpha_l(t_i)$ derived from samples. For this fitting, the stationary case of r(t) in equation (3.15) produced the highest determination coefficient, a value of $R^2 = 0.84$. A statistical analysis of the residuals show normality (χ^2 $p > 0.05$) and homoscedasticity (Fisher F=1.6 test p=0.23). This means that there was good correspondence between the observed and fitted values (Fig. 1)

The estimated form of $r(t)$ obtained in the fitting of equation (3.14) was substituted into equation (3.8) to get an estimated form of the environmental scaling factor $ø(t)$. Monthly leaf-growth rates were then projected by using equation (3.6) (Fig. 2). The associated variances projected through equation (3.7) are shown in Fig. 3. The observed monthly values for the MLGR produced an overall daily average of 10.9 *mm* day^{-1} leaf^{-1} with a standard error of 0.53 *mm* day^{-1} leaf^{-1}. The corresponding projected values produced an average of 10.2 *mm* day^{-1} leaf^{-1} with an associated standard error of 0.56 *mm* day^{-1} leaf^{-1}. We performed a χ^2 test and found no differences (p=0.997) between observed monthly averages and the

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 56 (3): 1003-1013, September 2008
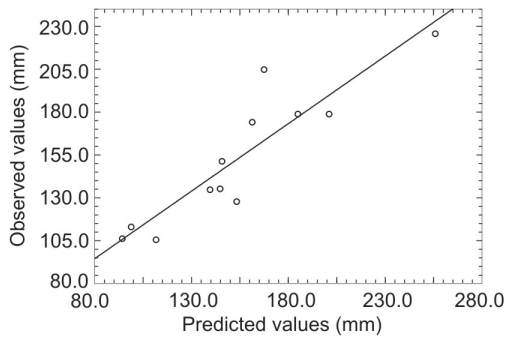
1007

Fig. 1. Predicted against observed values for the fitting of equation (3.14) with resulting $R^2 = 0.84$. This fitting produced the estimated parameters for the representation of $r(t)$ and $s(t)$ as given in equations (3.15) and (3.16). Fitted parameter values for s(t) were $a_{x0} = 1.4$, $a_{s1} = 0.08$, $a_{s2} = -0.08$, $b_{s1} = -0.04$, $b_{s2} = 0.03$ and $c_s = 3.2$. For r(t) a stationary representation produced $a_{r0} = 0.86$ with the highest determination coefficient. The estimated forcing factor $ø(t)$ obtained by replacing the identified form of $r(t)$ into equation (3.8) produced, through the use of equation (3.6), the projected rates in Fig. 2.
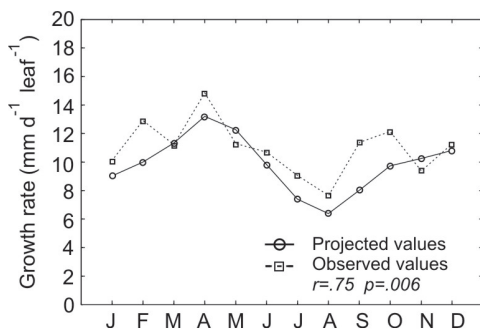

Fig. 2. Projected and observed mean daily leaf growth rates through time. These projections were obtained by substituting the estimated form of $ø(t)$ into equation (3.6), using available leaf-length data. The suitability of both model (3.2) and the sample based estimation of l_∞ can be used to explain the differences between observed and projected values. Both time series have the same statistical properties, which was corroborated by means of a χ^2 test.

corresponding values projected through equation (3.6).

Application to an independent data set: Cabello-Pasini *et al.* (2002) evaluated the effects of storms on photosynthesis, carbohydrate
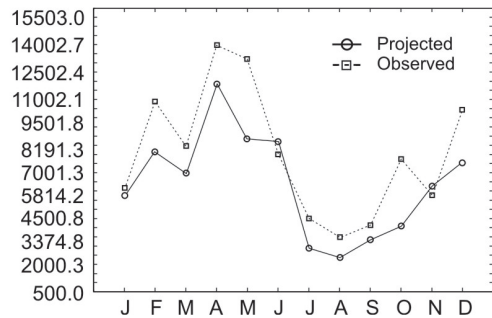

Fig. 3. Projected and observed monthly variance values for mean growth rates. The projected variances were calculated by means of equation (3.7) using leaf-length data and the identified form of $ø(t)$.

content and survival of seagrass at Punta Banda estuary and estimated a value of $4.8\pm0.8\%$ d^{-1} as the average specific leaf-growth rate. Using their leaf-length data and the estimated form of the environmental factor $ø(t)$ determined from our data, we projected the corresponding MLGR through equation (3.6) and obtained a specific growth rate of 4.2 ± 0.02 mm day^{-1}. This result shows that our analytical projection method gives consistent results when applied to data from similar *Z. marina* meadows.

Application to transplanted plot data: the projection method was also used to estimate MLGR for an experimental transplant at our study site. Removal of shoots was necessary four months after planting due to an infestation of the bryozoan *Zoobotrion verticillatum* which dramatically reduced light availability in the water column (Solana-Arellano *et al.* 2002). Using the fitted form of $ø(t)$ and the corresponding average leaf length, we projected a mean leaf growth rate of 14.4 *mm* day^{-1} leaf^{-1} for this transplant. This value was similar to the maximum monthly observed rate in the natural population (Fig. 2). Moreover, the allometric model of Solana-Arellano *et al.* (1998), which expresses leaf-dry weight in terms of the corresponding area, was fitted to the harvest data. No significant differences were found in the scaling parameters with respect to leaves

1008

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 56 (3): 1003-1013, September 2008

growing in the natural meadow. This result, along with a consistent value for MLGR, suggests that the transplanted shoots were growing in the same manner as those in the natural environment.

DISCUSSION

Most of the methods used to study growth and production in marine phanerogams are expensive, time consuming, and require destructive techniques such as leaf marking (Sand-Jensen 1975, Jacobs 1979). Excessive manipulation of raw material also increases the error introduced into the data (Mandel 1964). Our indirect estimations, which we call analytical projections, are based on measurements of leaf length and a scaling factor associated with environmental forcing. This factor can be obtained directly from observed leaf-length data using regression procedures. Hence, the resulting characterizations can reduce research expenses by simplifying assessment techniques.

The analytical assessment method introduced here was adapted from the model of equation (3.2), which has the advantage of linearity (i.e, the individual leaf growth rates depend linearly on leaf length). This property assures that the asymptotic growth assumption is maintained for the corresponding averages. Another feature of the linearity in equation (3.2) is its implied structural stability. That is, small perturbations in either the forcing function $ø(t)$ or the parameter l_∞ will produce small deviations in the projected MLGR values.

The deviations between projected and observed values in Fig. 2 can be explained in terms of both the determination coefficient of the fitting and also on the suitability of the estimated value for l_∞. Whenever the fitting of equation (3.13) fails to be robust, and the estimation of l_∞ is not representative of its true value, equation (3.8) will fail to produce realistic values for the forcing factor $ø(t)$. In those cases, the projection is not expected to represent the general properties of the observed time series. Our analytical method is thus highly sensitive to the adequacy of the asymptotic

growth assumption of model (3.2). Moreover, the sampling design must provide a representative stream of leaf-length data, which is crucial for a sound identification of the asymptotic length. Thus, the time-scale of observation is an important issue for the identification task and for the reduction of degrees of freedom. These provisions should afford a sound basis for the identification of both l_∞ and the environmental scaling factor $ø(t)$

Because Z. *marina* shoots are renewed about once a year (Olesen and Sand-Jensen 1994), this time span of observations provides for the proper estimation of the asymptotic length, as well as sufficient data for the fitting of equation (3.14). To achieve this step, we relied on data for whole leaves as required by the asymptotic growth assumption. Although incomplete leaves could be used to measure elongation between sampling dates, and therefore provide an accurate statistic of mean leaf-growth rate, this will fail to identify the size of the leaf relative to the asymptotic length in an unambiguous way. This is a fundamental entry in all asymptotic growth models, since the closer the leaf is to the asymptotic length, the smaller its growth rate is expected to be. Further, Ibarra-Obando and Boudouresque (1994) and Ibarra-Obando *et al.* (1997) have stated that the use of whole leaves should allow a better identification of seasonal trends, which affect leaf growth and shoot morphometrics in eelgrass. Hence, it was assumed that the use of whole leaves permitted a more realistic characterization of the environmental forcing factor $r(t)$.

The observed time series of mean leaf-growth rates is a sample path of an underlying causal stochastic process (Hoel *et al.* 1972). In that sense, the projected time series must have the same statistical properties, including the same expected value, over the whole sample space. To test this we performed a χ^2 test, which indicated no significant differences between observed and projected values. We also found a remarkable consistency in the projected value for the annual average rate of leaf growth, which was virtually the same as the one

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 56 (3): 1003-1013, September 2008

1009

we calculated from field data. Moreover, using leaf-length data in Cabello-Pasini *et al.* (2002), we projected the corresponding specific growth rates and found a good correspondence with the mean reported by those workers. The application of our projection method to the transplant experiment data in Solana Arellano *et al.* (2002) permitted us to obtain a non-destructive characterization of the associated MLGR and to infer about differences in growth parameters between the transplanted and the natural populations. This provides another example of the advantages of the method for indirect estimation methods presented here.

Hence, we conclude that our indirect estimation method is expected to be particularly useful for protected or transplanted areas where the effects of sampling could be deleterious. For natural populations where the effect of sampling may not be an issue, our constructs could simplify the traditional estimation procedures based on leaf marking techniques. Moreover, our method could be successfully applied to other seagrass species which have leaf growth dynamics similar to eelgrass, where leaf width can be considered as roughly constant after an initial growth stage.

Since *Z. marina* is a temperate-climate species, it is reasonable to expect that values of standing-stock variables will be higher during La Niña (cooler water) than El Niño (warmer water) events. For example, Ibarra-Obando and Huerta-Tamayo (1987) reported an average mean leaf-growth rate of 8.4 mm d^{-1} on the basis of data obtained at San Quintín Bay (an estuary 100 km south of our study site) during 1982, one of the strongest ENSO events reported to date, when annual mean sea-surface temperature was 20 °C (http://ingrid.ldeo.columbia.edu/SOURCES/.CAC/.sst/). Using our method, the corresponding projected values is 10.2 mm d^{-1}. Also for San Quintín Bay, Ibarra-Obando *et al.* (1997) reported averages of 85.03 mm for leaf length and an average leaf dry weight of 0.01 g during the ENSO event of 1987 when annual mean sea-surface temperature was 18.4°C. Our estimates of these variables were 1.54 mm and

0.015 g, respectively. It should be noted that the data used in this study were obtained in 2000, a year that presented negative sea-surface temperature anomalies and annual mean temperature was 16.4ºC (http://ingrid.ldeo.columbia.edu/SOURCES/.CAC/.sst/).

For leaf turnover, Ibarra-Obando *et al.* (1997) reported a value of 9.7 yr^{-1}. Other authors have found similar values in other eelgrass populations (Duarte 1991). Short eelgrass turnover times may have induced a short delay response to more favorable, cooler sea-surface temperatures, in such a way that the larger values in our data can be explained. Differences between standing-stock data presented in this study and similar variables published by other workers are likely the result of differences in sea-surface temperatures during the periods sampled (Short and Neckless 1999). Thus, comparison of our standing-stock data with previously reported assessments suggest the significant forcing effect of sea-surface temperature on eelgrass leaf dynamics.

Global climate change is expected to result in reduced productivity of seagrasses because of higher sea-surface temperatures. Moreover, accelerating economic development along the coastline of the US-Mexico border region assures continued human impacts on seagrass communities. The importance of these ecosystems will certainly promote restoration efforts, and the monitoring of such projects will require the design of cost-effective and non-destructive procedures (Phinn *et al.* 1999). This paper is aimed at contributing towards that objective.

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1010

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 56 (3): 1003-1013, September 2008

RESUMEN

Las praderas de pastos marinos abaten la erosión y aportan gran parte de la productividad primaria de los esteros y son refugio de muchos peces y sus larvas. El presente trabajo introduce métodos analíticos para estimar las tasas medias de crecimiento foliar de *Zostera marina* L. y sus varianzas. La calibración del método se llevó a cabo utilizando datos de una pradera de esta fanerógama en el Estero de Punta Banda Baja California, México. Las referidas estimaciones analíticas, se basan en medias de longitud foliar y en procedimientos estandarizados de regresión. Dichas determinaciones son por ende no-destructivas. Se proporciona una explicación detallada de los aspectos formales de la derivación del método. El valor promedio observado de la tasa media diaria de crecimiento foliar fue de 10.9 mm d^{-1} $leaf^{-1}$. El valor correspondiente proyectado mediante nuestro método fue de 10.2 mm d^{-1} $leaf^{-1}$. Los errores estándar asociados fueron 0.53 y 0.56 mm d^{-1} $leaf^{-1}$ respectivamente. Valores proyectados de la tasa media de crecimiento foliar diario utilizando datos de longitudes foliares publicadas por otros autores dieron también resultados consistentes. Se ilustra también el uso del método para proyectar la media de crecimiento foliar de una parcela transplantada de *Zostera marina.* La comparación de los resultados de este estudio con equivalentes reportados previamente nos permite concluir que las diferencias observadas pueden ser explicadas en función de la variabilidad de la temperatura superficial del mar en virtud del control de esta variable sobre la dinámica foliar de *Z. marina.* Las herramientas de estimación indirecta presentadas en este trabajo pueden aplicarse fácilmente a datos equivalentes de *Z. marina.*

Palabras clave: *Zostera marina,* tasa de crecimiento foliar, estimaciones analíticas.

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Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 56 (3): 1003-1013, September 2008

1011

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1012

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 56 (3): 1003-1013, September 2008

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Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 56 (3): 1003-1013, September 2008

1013