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Characterisation of environmental forcing on *Zostera marina* L. plastochrone interval dynamics in the Punta Banda Estuary, B.C. Mexico: an empirical modelling approach

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SUMMARY: This paper presents a characterisation of the most significant environmental influences on plastochrone interval variation for *Zostera marina* L. in Punta Banda estuary B.C. Mexico. Data were collected from April 1998 to December 2001. Using correlation and principal component analysis, we found that the combination of sea surface temperature, light radiation and dissolved nutrients explains the observed variability consistently. Sea surface temperature was found to be the dominant environmental influence (r=0.89, p<0.05). Using empirical modelling procedures we also found that there is **a** direct causal relationship between sea surface temperature and plastochrone interval values. In conclusion, from both a quantitative and a qualitative perspective sea surface temperature was found to summarise the relevant environmental forcing. Moreover, ENSO events control plastochrone interval variation throughout alterations in abiotic variables determining the observed dynamics.

Keywords: empirical modeling, eelgrass plastochrone interval, temperature control.

RESUMEN: Caracterización del forzamiento ambiental sobre la dinámica del intervalo de plastocrono en *Zostera marina* L. en el estuario de Punta Banda B.C. México: una aproximación de modelado empírico. – En este artículo se presenta una caracterización de las influencias ambientales mas importantes sobre la variación del intervalo de plastocrono para *Zostera marina* L. en el estuario de Punta Banda B. C. México. Los datos fueron recogidos de abril de 1998 a diciembre de 2001. Utilizando análisis de correlación y análisis de componentes principales se encontró que una combinación de luminosidad, temperatura superficial del mar y nutrientes disueltos explica la variabilidad observada de una manera consistente. La temperatura superficial del mar es el factor dominante (r=0.89, p<0.05). Mediante procedimientos de modelación empírica, se demostró que existe una relación causal directa de la temperatura superficial del mar sobre los valores del intervalo de plastocrono. Se concluye que tanto a nivel cuantitativo como cualitativo la temperatura superficial del mar totaliza adecuadamente el forzamiento ambiental pertinente. Más aún, las alteraciones en las variables abióticas asociadas con eventos ENSO determinan la variabilidad observada en el intervalo de plastocrono.

Palabras clave: modelación empírica, intervalo de plastocrono de *Zostera marina*, control de temperatura.

INTRODUCTION

Extensive beds of the seagrass *Zostera marina* L. (eelgrass) are commonly found in soft sediments in shallow areas of estuaries. Eelgrass provides important environmental services such as a habitat or shelter for many fishes and fish larvae, a substrate for attached algae or epifauna, and phytoremediation of contaminated sediment (McRoy, 1966; Williams *et al.,* 1994). In spite of its primary ecological im-

portance, anthropogenic influences have threatened the health of eelgrass and other seagrasses to such an extent that special conservation efforts of these ecosystems are nowadays required. Duarte (2002) considers that one important key action for conserving and restoromg seagrass ecosystems is the development of quantitative models predicting the response of seagrasses to disturbance.

In the development of analytical methods for expanding our knowledge of seagrass ecosystems, empirical models have played an important role, even before Fredrick T. Short introduced the first simulation model to study eelgrass growth (Short, 1975, 1980). In these contributions, light limitation was modelled through an adaptation of the Steel (1962) paradigm for plankton dynamics. A second limiting factor linked to the influence of current speed on distribution and production was empirically derived from experimental data. Temperature as a third limiting factor was also represented by means of an empirical relationship. A number of additional reports demonstrate that empirical modelling has contributed to seagrass research, in validation of theories, enumeration of phenomena, data organisation and prediction within relevant data ranges (e.g. Short, 1980; Duarte, 1991; Zimmerman *et al.,* 1991; Duarte and Chiscano, 1999; Zharova *et al.,* 2001; Best *et al.,* 2001; Greve and Krause-Jensen, 2005). In particular, Costa (1988) used a fourth order polynomial to generate a plastochrone interval curve for estimating eelgrass production in Buzzards Bay (USA). In the present contribution we introduce a generalised framework for the empirical characterisation of environmental influences in plastochrone interval dynamics for eelgrass in our study site.

The use of leaf-marking techniques and the development of a plastochrone index (PI) (Erickson and Michelini, 1957) provide information applicable to many seagrasses. For instance, for metabolic or physiological measurements, samples can be standardised in terms of the PI to reduce within-treatment variation (Dennison, 1980). Plastochrone methods are also used for measuring growth in many species based on the time interval between the production of new plant parts and the size of a mature leaf (Short and Duarte, 2001). Plastochrone interval assessments can be applied to determine shoot age, so this index is extremely important in the demography of seagrasses (e.g. Kraemer and Alberte, 1993; Van Tussenbroek, 2002).

Direct plastochrone interval estimations for *Zostera marina* were presented for the first time, in Sand-Jensen (1975). Jacobs (1979) introduced an explicit formula for estimating the aforementioned index. This defined a PI as the ratio given by the number of marked shoots times the observation period in days, divided by the number of new leaves on marked shoots (see Equation (1)). Values of the PI calculated through this formula produced estimations for shoot, leaf sheath, root and rhizome production rates. Other applications of the PI to eelgrass are found in Kraemer and Alberte (1993), who used this index to correlate age of shoots with metabolism and biomass. Also, Gaeckle and Short (2002) developed a plastochrone method for measuring leaf growth. This method provides a way to simplify assessments by relating leaf growth per shoot to the weight of the third leaf divided by the plastochrone interval. These authors considered that due to environmental influences the plastochrone interval must be measured for each growth determination. Other authors have also pointed out that the elucidation of environmental influences on PI variation is an important research problem (Durako, 1995; DiCarlo, 2004). This contribution includes one of the largest sets of time series data on PI variation that has been reported. This, in combination with the empirical tools, produced a consistent characterisation of the relevant environmental forcing.

Primary abiotic factors influencing eelgrass dynamics are temperature, light radiation, dissolved nutrients, substrate composition, dissolved oxygen, salinity and water movement. Salinity and substrate composition are key factors controlling distribution (Selig *et al.,* 2007). Salinity could induce osmotic stress and alterations in plant susceptibility to disease (Biebl and McRoy, 1971; Short and Neckles, 1999). Light and temperature influence distribution, density, flowering, biomass, and production (Mukai *et al.,* 1980; Phillips and Backman, 1983; Dennison and Alberte, 1985; Bulthuis, 1987). Dissolved oxygen, inorganic nutrients (including carbon) and water movement modify photosynthetic characteristics. While light, temperature and dissolved oxygen regulate instantaneous photosynthetic rates, the availability of inorganic nutrients affects the long-term response of photosynthesis by controlling the levels of photosynthetic enzymes and pigments (Solana-Arellano *et al.,* 1997).

In the study of environmental influences on eelgrass, one must take into account a certain level of colinearity among most of the considered primary abiotic factors and sea surface temperature. In fact, the solubility of oxygen or its ability to dissolve in water decreases as the water temperature and salinity increases (Odum and Odum, 1959; Yin *et al.,* 2004). Moreover, variation in sea level caused by thermal expansion of the water column can induce changes in underwater light radiation, modify tidal variation and alter water movement (Short and Neckles, 1999). The more significant these colinearity linkages are, the grater the control of sea surface temperature on eelgrass dynamics is expected to be. Solana-Arellano *et al.* (1997) and Echavarria-Heras *et al.,* (2006) corroborated these effects and found that sea surface temperatures control the dynamics of eelgrass leaf elongation and associated variables in an essential way.

We performed a correlation analysis between obtained PI values and sea surface temperatures (SST), air and underwater radiation, salinity, phosphate and nitrate concentrations in the water column and in interstitial water. In order to characterise the relative importance of these environmental factors, we used a principal component analysis (PCA). We found that the dynamics of observed PI values is dominantly driven by SST. The use of empirical modelling methods derived from a Taylor's theorem representation (cf. Equation (3)) allowed us to consistently relate the observed dynamics with the large-scale environmental influence of the ENSO events. Furthermore, these empirical methods provided a qualitative basis for establishing a decisive causal linkage between SST and the addressed dynamics.

MATERIALS AND METHODS

Study site

The data used for this study were collected in a *Zostera 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). The climate is characterised by warm summers and cool moist winters. Normally evaporation exceeds precipitation but extreme winter storms can drive freshwater input to exceed evaporation. This makes the estuary a permanent hypersaline environment where water renewal is essentially controlled by tides. Depth decreases from the mouth (12.5 m Mean Low Water (MLW)) to the head (1 m MLW) of the estuary, while water temperature and salinity increase. The residence time of water is slow near the mouth and decreases toward the head. Currents are tidally driven and generally <0.15 m s^{-1} (Pritchard *et al.,* 1978). Water transparency decreases consistently towards the head. Relatively low temperature and nutrient-rich upwelled waters from the adjacent oceanic region are carried to the area contiguous to the mouth of the estuary and tidal currents transport these waters to the interior. Nutrient remineralisation (Smith *et al*., 1991) at the sediment, as well as, the effect of turbulence induced by tidal currents and winds increase nutrient concentrations in surface waters.

Data acquisition and processing

Using the Kentula and McIntire marking technique (1986), about 40 shoots were marked biweekly from April 1998 to December 2001. Every two weeks, previously marked shoots were removed and a new set of shoots was marked. The collected shoots were placed in a portable cooler before being processed in the laboratory. We recorded the number of recovered shoots and counted the number of leaves present and the number of new leaves on shoots. Temperature and light radiation were permanently measured at the sampling site with a PAR and direct beam measuring Quatum Radiometer-Photometer (Li-Cor, Inc.) using an integration time of 1000 s. Salinity and nutrient concentration (phosphates and nitrates) were obtained biweekly from November 1999 to April 2001 (Fig. 1). Nutrient concentration data was obtained by the general technique of flow injection analysis (FIA) by the analytical lab in the Marine Science Institute of the University of California at Santa Barbara.

The average plastochrone interval values $PI(t)$ associated with a sampling date t were calculated through the formula:

$$PI(t) = \frac{MS(t)T(t)}{NLS(t)}, \qquad (1)$$

where $MS(t)$ is the number of recovered marked shoots in an observation period of length $T(t)$ in days, and $NLS(t)$ is the number of new leaves on recovered shoots (Jacobs, 1979). $T(t)$ was maintained unchanged throughout the study and amounted to two weeks.

Statistical analysis

We carried out a correlation analysis among abiotic variables and PI values. The included environmental factors were salinity, maximum, minimum and average temperature, underwater and air radiation, water column phosphate and nitrate concentrations and in interstitial water. In order to show which variables explain the variability of others, we applied a PCA among the above-mentioned forcing agents. All the statistical analyses were performed using STATISTICA (2006).

Empirical modeling tools

Assuming colinearity, we can produce a dynamical characterisation of the influence of a dominant environmental variable $\theta(t)$ on the observed $PI(t)$ values. A causal relationship between $PI(t)$ and $\theta(t)$ can be formally expressed by means of a continuous and differentiable function $f(\theta(t))$ such that the equation

$$PI(t) = f(\theta(t)) \qquad (2)$$

holds. Assuming that $f(\theta(t))$ has continuous derivatives of all orders, we can apply Taylor's theorem (Fulks, 1978) and obtain a representation,

$$PI(t) = \sum_{k=0}^{n} a_k \theta(t)^k + R_n \quad , \qquad (3)$$

where for $0 \le k \le n$, ak is a parameter expressed in terms of the kth order derivative of $f(\theta(t))$ and Rn a remainder. A goodness of fit analysis for Equation (3) determines the extent to which a given variable $\theta(t)$ explains the dynamics of the $PI(t)$ values.

RESULTS

Figure 1 shows the environmental variables measured in our study. We can see marked differences among years in all variables. Seasonal and interannual variability is described in Solana-Arellano (2004). From the correlation analysis, only salinity estimations resulted in a low correlation coefficient ($r \le 0.30$, $p=0.25$), so this variable was dropped out from a further PCA (Tabachnick and Fidell, 2001). We found three principal components describing PI

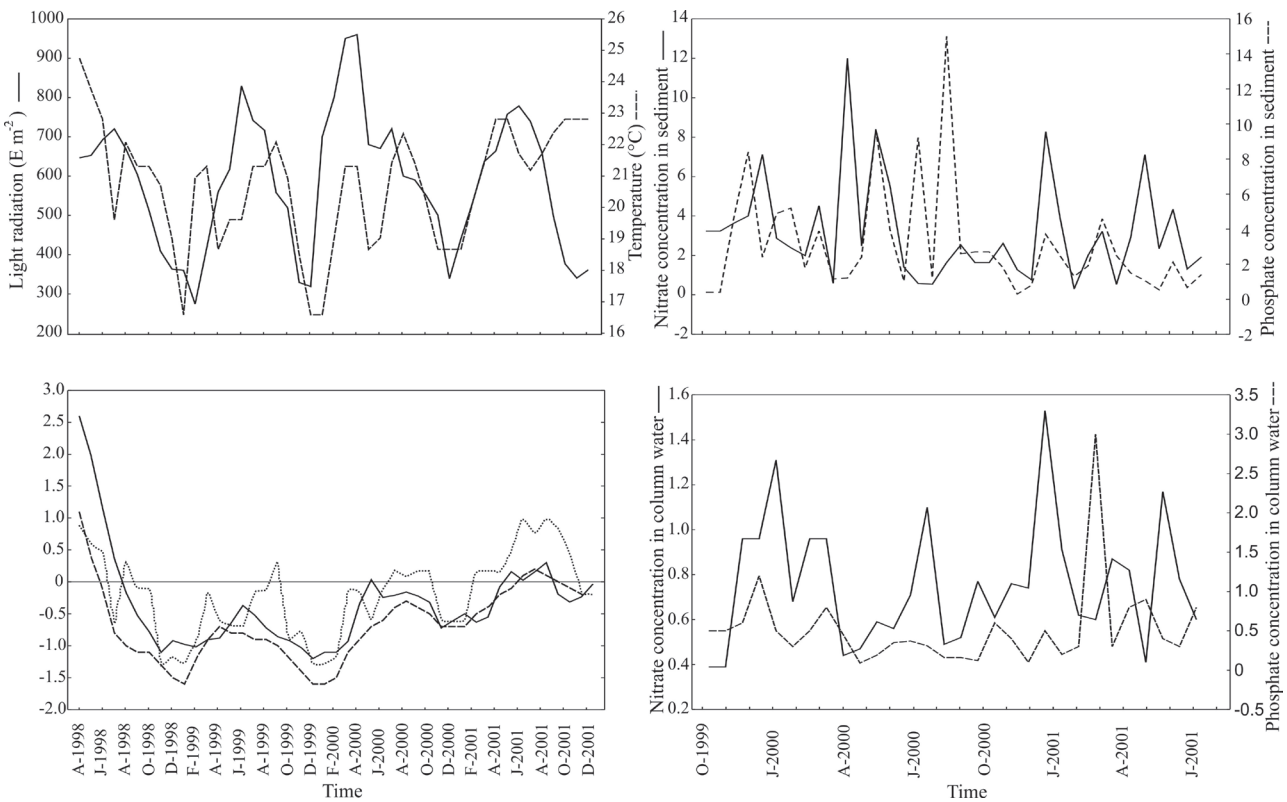

FIG. 1. – Measured environmental variables. a) Light radiation and temperature. b) Phosphate and nitrate concentrations in sediment. c) The continuous line represents the time series of MEI values. Small dashed line symbolises the ONI values. Sea surface anomalies values are represented in large dashed line. d) Phosphate and nitrate concentrations in sediment in column water.

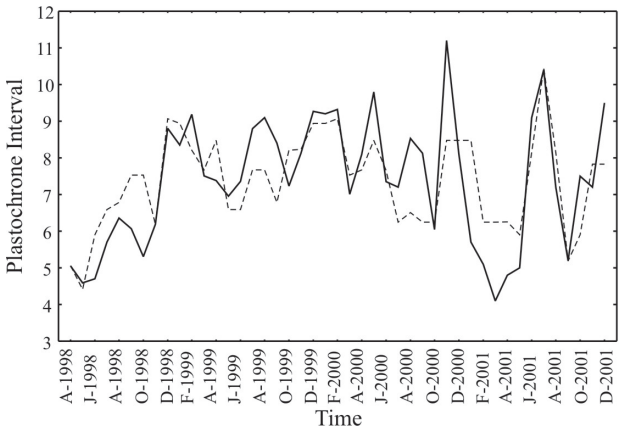

FIG. 2. – The continuous line represents plastochrone interval estimations taken biweekly over a 45-month observation period. The dashed line represents a fitting of Equation (3) to the observed plastochrone interval values. In this case, $\theta(t)$ represents in situ surface temperature anomalies and produced a determination coefficient of R^2=0.73. The best fit corresponded to the case n=25. For $P(t)$ standing for observed plastochrone interval values the fitted model is given by:

$$P(t) = 6.55 - 5.7\theta(t) + 6.31\theta(t)^2 + 255.5\theta(t)^4 - 3110.3\theta(t)^6 - 412\theta(t)^7 + 6174.6\theta(t)^8 + 801\theta(t)^9 - 9027.4\theta(t)^{12} - 5506\theta(t)^{13} - 4879\theta(t)^{20} + 1.8\theta(t)^{21} - 3425.2\theta(t)^{22} + 1282\theta(t)^{23} - 986.3\theta(t)^{24}$$

values. The first principal component is mainly described by maximum (r=0.86, p<0.05) and average (r=0.89, p<0.05) temperature and explains 30% of PI variability. A second principal component is composed of minimum temperature (r=0.75, p<0.05) and explains 20% of PI variability. The third principal component is mostly described by phosphate concentrations in the water column (r=0.79, p<0.05) and explains 16% of PI variability. It turned out that while temperature explained 50% of PI variability, light radiation was excluded from all these principal components ($r \leq$-0.52, p=0.05). This shows that among the considered variables, measured SST is the dominant factor for the addressed PI variation. In order to explore intermediate and large-scale temperature forcing we performed a correlation analysis among plastochrone interval series, in situ sea surface temperature anomalies, the multivariate ENSO Index (MEI) and the Oceanic Niño Index (ONI) values. We found that all these variables have significant correlations with the PI values ((-0.57, p<0.02), (-0.42, p<0.000) and (-0.45, p=0.000) respectively). Moreover, these variables were found to be highly correlated with each other, with correlations ranging from 0.65 to 0.84 (p<0.05 for all). We also performed a correlation analysis between PI values and temperature and light radiation values lagged up to six months. The results of the analysis showed no significant correlations between PI and any of the lagged light radiations values (p>0.40).

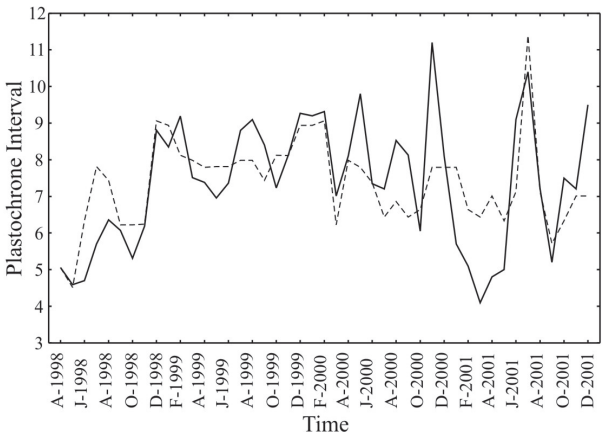

FIG. 3. – The continuous line represents plastochrone determinations through time. The dashed line was produce by the fitting of Equation (3) to these plastochrone interval values. In this case, $\theta(t)$ stands for ONI values. The best fit was obtained for a polynomial of order 25 with a determination coefficient of R^2=0.70. ONI values are based on three-month running-mean SST departures from average (Smith and Reynolds, 2003). For $P(t)$ standing for observed plastochrone interval values the fitted model is given by:

$$P(t) = 5.7 + 0.67\theta(t) + 105.2\theta(t)^2 + 356.3\theta(t)^3 - 376.3\theta(t)^4 - 2532.6\theta(t)^5 - 1839.6\theta(t)^6 + 1328.9\theta(t)^7 - 62.3\theta(t)^8 - 1029.9\theta(t)^9 + 1376.7\theta(t)^{10} - 345.8\theta(t)^{11} - 380.8\theta(t)i^{12} + 1316.7\theta(t)^{13} - 779.5\theta(t)^{14} + 398.2\theta(t)^{15} + 954.7\theta(t)i^{16} - 859\theta(t)^{17} + 968.8\theta(t)i^{18} + 658.6\theta(t)^{19} - 768.6\theta(t)^{20} + 1125\theta(t)^{21} + 116.3\theta(t)^{22} - 829.4\theta(t)^{23} - 943.1\theta(t)^{24} - 219\theta(t)^{25}$$

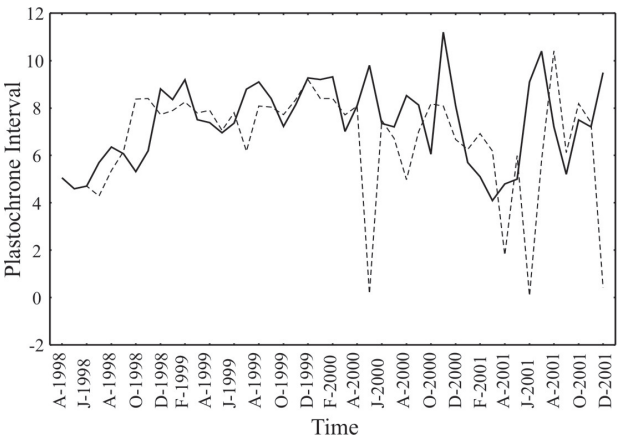

FIG. 4. – The continuous line shows plastochrone intervals determined through time. The dashed line corresponds to equivalent values fitted through Equation (3) and the variable $\theta(t)$ was characterised by MEI values through time. The best fit was obtained for n=15 and produced a determination coefficient of R^2=0.58. MEI index corresponds to a multivariate measure of the ENSO signal as expressed in the first component of six observed variables: sea level pressure, surface zonal and meridional wind components, sea surface temperature, surface air, temperature and cloudiness (Wolker and Timlin, 1993). For $P(t)$ standing for observed plastochrone interval values the fitted model is given by:

$$P(t) = 8.3 + 3.2\theta(t) - 18.1\theta(t)^2 - 33.4\theta(t)^3 + 17.9\theta(t)^4 - 17.2\theta(t)^5 + 56\theta(t)^6 - 17.2\theta(t)^7 + 21.9\theta(t)^8 - 19.2\theta(t)^9 + 56.9\theta(t)^{10} - 25.1\theta(t)i^{11} - 65\theta(t)^{12} + 21\theta(t)^{13} + 17.2\theta(t)^{14} - 5.9\theta(t)i^{15}$$

Similarly, PI values showed no significant correlations with lagged temperature (p>0.07), so no lags were considered in the analysis throughout.

Equation (3) was fitted to the $PI(t)$ time series, letting $\theta(t)$ represent either locally obtained sea sur-

face temperature anomalies or the addressed ENSO indexes. Figure 2 corresponds to the fitting of $PI(t)$ values to $\theta(t)$ standing for *in situ* sea surface temperature anomalies. The best fit was obtained for n=25, and the associated determination coefficient was of R^2=0.73. Figure 3 displays the fitting of Equation (3) for $\theta(t)$ representing ONI values (Smith and Reynolds, 2003). The best fit was obtained for n=25, and the corresponding determination coefficient was R^2=0.70. Finally Figure 4 presents the results of the fitting of Equation (3) for the case in which $\theta(t)$ correspond to MEI values (Wolker and Timlin, 1993). For this fit the determination coefficient was R^2=0.58 and corresponding to n=15.

DISCUSSION

Most seagrasses are composed of long-lived individuals rooted in sessile habitats. They are sensitive to environmental conditions to such an extent that growing conditions are recorded in their tissues, growth form and distribution patterns (Fourqurean *et al.,* 1997), and these characteristics allow them to be effective integrators of environmental conditions. Furthermore, temperature and irradiance induce a seasonal variation for the dynamics of most seagrasses (Sand-Jensen, 1975; Olesen and Sand-Jensen, 1994; Guidetti *et al.,* 2002; Sang *et al.,* 2006 among others). Particularly, for eelgrass growth dynamics is highly correlated with sea surface temperature (Short and Neckles, 1999; Solana-Arellano *et al.,* 1997; Solana-Arellano *et al.,* 2004). According to Setchel (1929), eelgrass can grow only within a fixed temperature range (0°C-38°C). Other authors (Rasmussen, 1977; Phillips and Backman, 1983) have also shown that temperature is fundamentally important in the control of the seasonal growth cycle of eelgrass. Light has been shown to influence its distribution (Dennison and Alberte, 1985), density (Mukai *et al.,* 1980), flowering (Phillips and Backman, 1983) and biomass (Mukai *et al.,* 1980; Bulthuis, 1987). It is also known that eelgrass can absorb nutrients either from the roots or the leaves (McRoy *et al.,* 1972). Hence, modifications in upwelling activity, stratification, and tidal dynamics could alter the availability of dissolved nutrients and thus affect eelgrass productivity (Echavarría-Heras *et al.,* 2006).

The present data on PI variation was obtained from a well established eelgrass population which is distributed in shallow areas of a hypersaline coastal lagoon where water currents are slow. Hence, at a first glance we can assume that the addressed dynamics is mainly determined by water temperature, incident and underwater light radiation, salinity and dissolved nutrients (Solana-Arellano *et al.,* 1997; Zharova *et al.,* 2001). The variability of these environmental influences is determined by a series of climatic and oceanographic events which take place over different spatial and temporal scales and are characteristic of the California Current System (CCS), with upwelling events that persist during the entire year and el Niño/Southern Oscillation (ENSO) events that induce alterations in most abiotic variables (Echavarria-Heras *et al.,* 2006). The results of this research show that environmental variability characterised by the action of temperature, irradiance and dissolved nutrients plays an important role in the control of new leaf formation in eelgrass at our study site. Together these variables explained about 70% of the variability of the observed PI data. Moreover, the performed PCA resulted in a highest correlation coefficient for sea surface temperature (r=0.89, p<0.05).

The statistical methods and empirical modelling tools used revealed the importance of colinearity effects among sea surface temperature and the other environmental variables that were considered. These effects were found to be significant enough to raise sea surface temperature as a crucial influence for the addressed dynamics. The fittings of Equation (3) corroborate that over the considered scales SST is the most significant causal influence for the observed PI dynamics. Furthermore, Figures 2 and 3 display smaller deviations between observed and predicted values than Figure 4. An explanation for this result lies in the fact that while for the fittings of Figures 2 and 3, $\theta(t)$ depended directly on SST anomalies, for the last fitting $\theta(t)$ was characterised by other environmental influences in addition to sea surface temperature anomalies, as it corresponds to the MEI index. This is determined as a multivariate measure of the ENSO signal, as expressed in the first component of six observed variables; sea level pressure, surface zonal and meridional wind components, sea surface temperature, surface air, temperature and cloudiness (Wolker and Timlin, 1993)

The use of Equation (3) was beneficial for the purpose of closing the gap between the descriptive information in our data and the quantitative information we have obtained. This permitted the elucida-

tion of the important contribution of ENSO events in the control of the addressed dynamics. In other words, this study shows that major influences like ENSO events leave a signature on eelgrass PI variation. In fact, within the CCS the El Niño/Southern Oscillation (ENSO) events represent positive and negative anomalies in sea level and surface temperature (Parés-Sierra *et al.,* 1997). These effects produce warming of local waters, change in the salinity, decrease in coastal upwelling, and anomalously high sea level (Durazo and Baumgartner, 2002). Effects on upwelling and sea level are related to nutrient and underwater light radiation availability (Echavarria-Heras *et al.,* 2006). As *Zostera marina* is a temperate-climate species, we could expect La Niña events (cold water) to cause an increase in eelgrass response variables, and El Niño events (hot water) to cause a decrease in them. 1998 is considered to be a strong "El Niño" ENSO event and 1999 to February 2001 is considered to be a "La Niña" event. Moreover, from March 2001 to August 2002 another strong "El Niño" event was recorded. An inspection of Figures 2 to 4 readily shows that PI dynamics is consistent with the above-quoted temperature control paradigm. Furthermore, we can assess that ONI values based on three-month running-mean SST departures from average (Smith and Reynolds, 2003) and on in situ SST anomalies provide a better goodness of fit criterion on MEI values. The influences of variables in addition to SST explain the relatively larger deviations in Figure 4. This is in agreement with our correlation and PCA findings, which sustain the fundamental control of SST over the observed dynamics.

Our results are consistent with the fact that SST has a great influence on marine ecosystem dynamics (Tegner and Dayton, 1987; Beer and Koch, 1996; Johnson *et al.,* 2003). Particularly for the estuarine environment, a change in temperature affects the many chemical processes taking place in plant or animal tissues and thus affects the entire ecosystem. In addition, many physical characteristics, such as viscosity, density and solubility of oxygen in water, are directly related to temperature. In estuaries, the heat-storage capacity is small relative to the large volume of the ocean, so temperature changes are closely correlated with seasonal climatic variation. This provides a conceptual framework for the detected colinearity effects that allowed SST to summarise the environmental influences on the observed PI dynamics.

The fact that among the considered environmental variables irradiance made a lesser contribution deserves further elaboration. In fact, a widespread belief asserts that 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; Orth and Moore, 1988; Zimmerman *et al.,* 1991). Hence, natural or anthropogenic influences that reduce incident radiation and/or increase estuarine turbidity are expected to have important effects on eelgrass dynamics. For the period in which our data was collected, incident light radiation followed the normal variation pattern observed for the site. Nevertheless, dredging at the mouth of the estuary was a systematic activity. Associated turbidity could be a factor explaining a relatively shallow distribution for eelgrass. Whatever additional effects can be associated with this permanent turbidity condition, they have not prevented the establishment of a stable population distribution for eelgrass at the site. As a matter of fact, *Zostera marina* has been claimed to have maintained a high production during periods of maximum turbidity and nutrient input in Chesapeake Bay (Kempt *et al.,* 1983). As occurs at our study site, a shallower distribution along with an absence of epiphytisim could certainly have favoured a greater exposure to direct light. Moreover, persistency over suitably long periods of light attenuation could explain the dominance of factors such as dissolved nutrients or SST over light radiation in the control of the observed PI dynamics.

The maintenance of oxic conditions in meristematic and below-ground tissues in seagrasses is important for the support of rapid growth, nutrient uptake by roots and translocation of nutrients and carbohydrates between roots and leaves (Smith *et al.,* 1988; Zimmerman and Alberte, 1996). Furthermore, the meristematic metabolic activity that leads to new leaf formation demands high amounts of oxygen for the support of cell division and growth (Brix and Sorell, 1969). Eelgrass follows a mono-meristematic leaf-replacing growth form. This is characterised by a continuous leaf tissue production at a combined basal leaf/rhizome meristem area (Sand-Jensen, 1975; Short and Duarte, 2001). Moreover, it has been demonstrated that dissolved oxygen accessibility is an important factor controlling meristematic production of new leaves in eelgrass (Greve *et al.,* 2003). Hence, oxygen availability is expected to play an important role in the control of the observed eelgrass PI dynamics.

Situations of low oxygen concentrations in the water column are not unusual in natural seagrass beds and are often accompanied by severe seagrass mortality (Frederiksen and Glud, 2006). Hartman and Brown (1976) demonstrated that the oxygen produced by photosynthesis is stored and recycled in the internal lacunal system of the maprophytes. Radial diffusion plays an important role as a transport mechanism for oxygen stored in the lacunal system to the intercalary meristem (Sand-Jensen *et al.,* 2005). Furthermore, the meristematic O_2 concentration in the water column is closely coupled to O_2 concentrations of the overlaying water column (Greve *et al.,* 2003; Pedersen *et al.,* 2004). Dissolved oxygen levels in an estuary vary seasonally with the lowest levels occurring in late summer when temperatures are highest (Odum and Odum, 1959; Yin *et al.,* 2004). These empirical facts, as well as the results of Greve *et al.* (2003) on the linkage between dissolved oxygen availability and production of new leaves in eelgrass, provide a sound explanation for the important SST forcing on the observed PI dynamics we have found.

In the review of Estes and Peterson (2000) on marine ecological research in seashore and sea floor systems, it is emphasised that one of the most pressing needs for future knowledge is an effective characterisation of the complex influences of temporal and spatial scales on ecological processes. The present contribution shows how the use of empirical modelling can contribute to the aforementioned views. Furthermore, the quantitative framework presented offers a consistent characterisation of both intermediate and large-scale environmental forcing for the eelgrass plastochrone interval at our study site.

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