Leaf dynamics and production of a *Zostera marina* bed near its southern distributional limit

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Abstract

Through biweekly census, from January to December 1987, leaf dynamics and production of a perennial, intertidal population of *Zostera marina* L., were studied near the southern distributional limit of the species (30°N) in Baja California, Mexico. Shoots had an average of 4.0 leaves, and 1.0 new leaf appeared every week. The average number of new leaves per shoot was highest from May to August, while the average number of leaves present per shoot peaked during the September–December period. A maximum leaf area index of 4.1 m^2 m^{-2} was recorded at the end of the summer. Growth and production were continuous during the year, and annual means were 10 m m^{-2} d^{-1}, and 0.9 g dry wt m^{-2} d^{-1} respectively, with peak values in September. Growth and production were positively correlated with light and water temperature. This southern population presents a summer condition (May to October) during which, values increase and reach their maximum, and a winter condition (November to April) with low values. Intertidal zone shoots are characterized by their small size and high dynamics, with an average plastochrone interval value of 8.2 days, an average lifetime of a leaf of 37.6 days, and an annual turnover rate of 9.71 yr^{-1}. Environmental stability apparently allows vegetative activity to proceed throughout the year. © 1997 Elsevier Science B.V.

Keywords: Leaf number; Shoot morphometrics; Leaf growth and production; Turnover rate; Environmental stability

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1. Introduction

Autoecological studies deal with the characteristics of populations of one species, and the relations of this species with the surrounding environment. However, den Hartog (1979) mentioned that ''it is self evident that the annual cycle of the dominant seagrass species regulates to a high degree the floral and faunal composition of a number of subordinate structural elements, particularly the epiphytic algae and their grazers''. The above statement explains why, when the community or ecosystem at a new location is to be described, the annual cycle of the dominant species needs to be included.

Because of their high biomass and productivity, the organic production of seagrasses has been well studied; however, their leaf dynamics has received less attention. This is the case of *Z. marina* L. (Potamogetonaceae) for which leaf dynamics information is scarce, as production studies make reference to one or several of the following variables: average number of leaves per shoot, total number of new leaves produced, leaf life span and defoliation rates, in most cases giving only one value on an annual or seasonal basis (Sand-Jensen, 1975; Jacobs, 1979; Nienhuis and de Bree, 1980; Sand-Jensen and Borum, 1983; Thorne-Miller and Harlin, 1984, etc.). We consider that the methods used previously have failed to provide a complete picture of the spatial and temporal trends in leaf dynamics of this species. A good example of the situation is given in the comment of Hamburg and Homann (1986): ''temporal trends of both the rate of leaf emergence and number of leaves per shoot were erratic''.

The Baja California populations of *Z. marina* represent the southernmost populations along the North American Pacific coast (den Hartog, 1970). In the northern portion of the peninsula, where water temperature fluctuates between 11 and 27°C (Alvarez-Borrego and Alvarez-Borrego, 1982), the perennial form can be found (Dawson, 1962; Ibarra-Obando and Huerta-Tamayo, 1987), while in the southern portion of the peninsula and in the Gulf of California, where seawater temperature varies between 12 and 32°C (Phillips and Backman, 1983), the annual form is characteristic (Ward, 1983; McMillan, 1983; Phillips and Backman, 1983). Pacific coast beds attract more than 20 000 brant in winter (Massey and Palacios, 1994), and some of these beds are presently threatened by the oyster growing industry.

This paper presents the results of the first eelgrass annual cycle study for the temperate region of the Baja California peninsula. It focused on describing leaf dynamics and production of the perennial form. During this study a new methodological approach was used (Ibarra-Obando and Boudouresque, 1994), which allowed the use of whole leaves to describe leaf dynamics and shoot morphometrics. Leaf pieces for growth and production analysis used the meristem as a reference point. Because seasonal trends in light and temperature are weak, it was hypothesized that there would not be strong trends in the analyzed biotic variables.

2. Methods

The study took place at San Quintin Bay (30°29′–30°30′N, 115°57′–116°01′W), which is described by Ibarra-Obando and Aguilar-Rosas (1985), and Ibarra-Obando and

Huerta-Tamayo (1987). Two important characteristics distinguish the eelgrass beds in San Quintin, compared with other Pacific coastal lagoons: (1) They occur at very shallow depths, exposing them to the air during low tide; and (2) they have an unusually high shoot density (Neuenschwander et al., 1979). It is known that depths of -0.10 and $+0.20$ m with respect to mean low low water (MLLW) represent the lower intertidal and the transition zone between MLLW and mean low water (MLW), respectively (Ibarra-Obando and Huerta-Tamayo, 1987). Therefore, they were used to characterize the intertidal zone. A transect was installed at each of these depths, and transects were treated as replicates.

The selected mudflat for this study was in a slightly more southern location than used by Ibarra-Obando and Huerta-Tamayo (1987). It is located in the west arm of the bay (Bahia Falsa), has an area of 4.8 ha and is partially covered with a dense bed of *Z. marina*. At each of the above mentioned depths, a transect (130 m long and 0.5 m wide) parallel to the shore was established. During every spring low tide between January and December 1987 both transects were sampled and in each one of them seven sampling units (0.5×0.5 m) were selected. Sampling was at random (using a random number table) without replacement. At each sampling unit, three vegetative shoots were randomly selected and marked following the leaf marking technique of Ibarra-Obando and Boudouresque (1994) for a total of 21 marked shoots per transect. Marking and harvesting were continuous throughout the year. All replicates from each transect were pooled for each sampling period.

In every visit to the site, water samples for temperature, salinity and dissolved nutrients analyses were taken in the main channel, in front of the bed, at 1 m depth during high tide. Water temperature was measured with a bucket thermometer (precision $0.1°C$), while salinity was assessed in the laboratory using the hydrometer technique (G.M. Manufacturing, New York) (precision 0.1‰). Nutrients were analyzed following Strickland and Parsons (1972). Water column nutrients were considered a more homogeneous proxy of the overall environment than interstitial waters in sediments, which typically are highly variable in nutrient composition (Solana-Arellano et al., 1977). Photon irradiance was measured at noon using an integration time of 1000 s with an Integrating Quantum/meter (Li-Cor).

Whole leaves were obtained after shoot dissection, and field information on the number of present, new and shed leaves was used in the following formula:

$$\text{new leaves}_t = \text{present}_t - \text{present}_{t-1} + \text{shed}_t$$

For every leaf, total length and average width (middle section of the leaf) were measured and used to assess the total leaf length per shoot, mean leaf width per shoot and the LAI (leaf area index, a value that represents the leaf area (m^2) per m^2 of substrate). Shoot density information was obtained from estimates of biomass in which all apical and lateral shoots in seven 0.04 m^2 quadrants per transect were harvested, placed in plastic bags and transported to the laboratory where they were counted (Poumian-Tapia, 1995). In total, about 7000 leaves were measured over the year.

Leaf growth and production were measured with the growth analysis technique described by Ibarra-Obando and Boudouresque (1994). With this technique the meristem (first node) is used as a reference point, resulting growth and production are assessed at

the basal portion of the leaves. Leaf pieces representing growth were measured and their dry weight assessed. Specific growth and production data were multiplied by shoot density values, in order to assess these variables for the whole bed. Production data were multiplied by 0.38 (Westlake, 1963) to express them in terms of carbon. The plastochrone interval (PI), the mean time interval between the appearance of two successive leaves in a shoot (Patriquin, 1973), and the average lifetime of a leaf were calculated.

Descriptive statistics were obtained with the Statistica for Windows Program (StatSoft, Tulsa, OK, USA). Data fitted a normal distribution and showed homogeneity of variances, so parametric statistics were used. Differences through time were analyzed
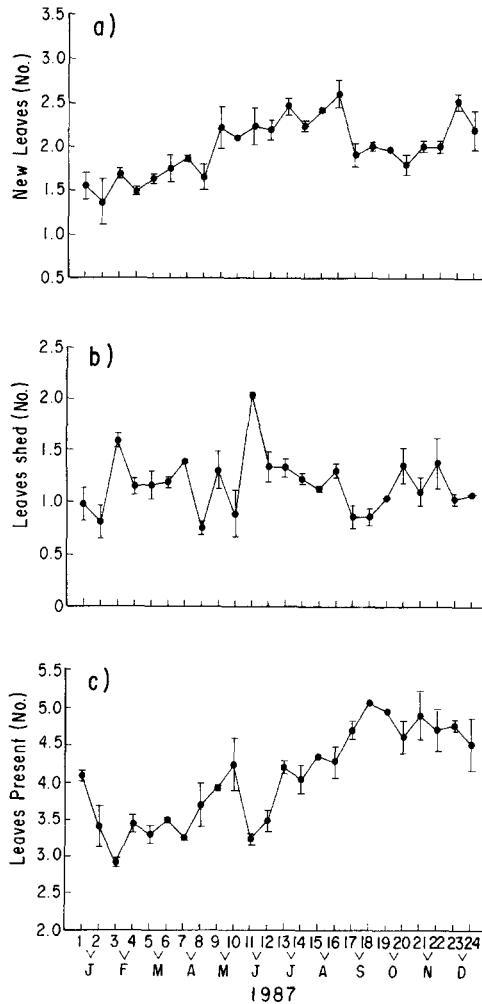

Fig. 1. Leaf dynamics annual variations. (a) Average number of new leaves per shoot; (b) Average number of leaves shed per shoot, and (c) Average number of leaves present per shoot. Biweekly data are shown starting the first half of January (1) and finishing the second half of December (24). Bars indicate ± 1 SE.

with a one-way ANOVA, and when significant differences were found, the least significant difference (LSD) test was employed. Principal components analysis (PCA) was performed to analyze relationships between variables (Biomeco Program, Groupe Biometrie, Centre L. Emberger, C.N.R.S., Montpellier, France). The PCA to analyze the interrelationship among leaf types and environmental variables had 25 individuals (24 active and one supplementary that corresponds to the mean value) and 9 variables (new, shed and present leaves, light, water temperature and salinity, nitrate, nitrite and phosphate). The PCA performed to analyze the relationship of growth and production with environmental variables had 25 individuals (24 active and one supplementary) and 8 variables (growth, production, light, water temperature, salinity, nitrates, nitrites and phosphates). For all tests, the significance level was set at 0.05.

3. Results

The average number of new leaves per shoot shows significant differences through time ($P = 0.003$). The post hoc test allowed the identification of a low values period, from January to April (average of 1.6 new leaves per two week interval), and a high values period, from May to August (average of 2.3 new leaves per sampling interval). A second peak is evident in December. The annual mean is 2.0 new leaves per two-week interval. The lowest value (1.4) corresponds to the second half of January, while the highest one (2.6) to the second half of August (Fig. 1a). The average number of leaves shed per shoot also showed significant differences through time ($P = 0.01$) and periods of low values alternate with periods of high values, without a clear trend (Fig. 1b). An annual mean of 1.2 leaves shed per sampling interval was found. Peak values of 1.6 (first half of February) and 2.0 (first half of June) were found to correspond to strong periods of wind (Ibarra-Obando, 1992). The average number of leaves present shows significant differences through time ($P = 0.00005$) with low values from mid-January to the first half of April (average of 3.3 leaves per shoot) and high values from September to December (average of 4.8 leaves). The lowest value corresponds to February (2.9 leaves per shoot) and the highest to September (5.1). The annual mean was 4.0 leaves per shoot (Fig. 1c).

Table 1
Significant correlations between leaf types and environmental variables, obtained with a PCA

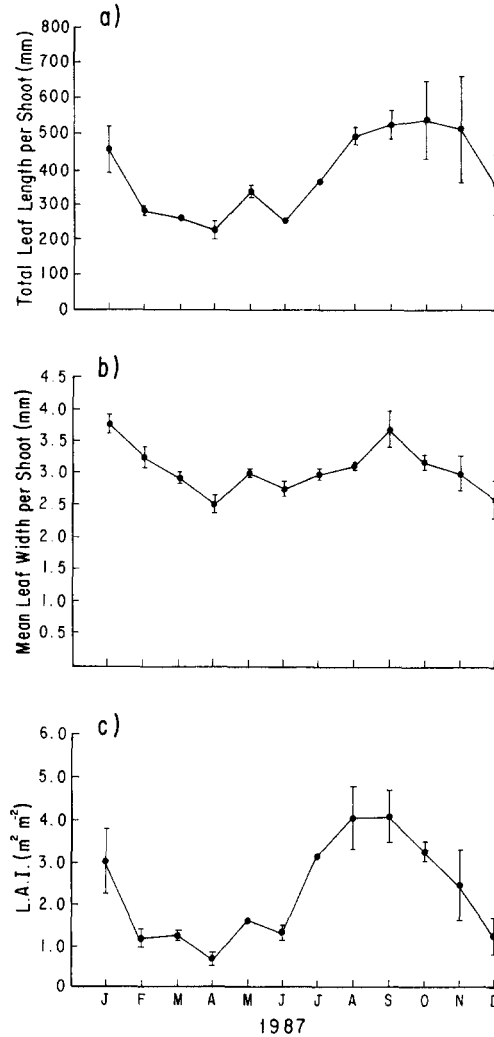| Variables	r	p
New leaves – phosphate	0.58	< 0.01
New leaves – nitrite	0.54	< 0.01
New leaves – water temperature	0.48	0.02
New leaves – leaves present	0.41	< 0.05
Leaves shed – salinity	0.41	< 0.05
Leaves shed – leaves present	−0.41	< 0.05
Leaves present – water temperature	0.55	< 0.01
Leaves present – salinity	−0.43	< 0.05
Nitrite – phosphate	0.45	< 0.05

Fig. 2. Monthly variations in shoot morphometrics. (a) Total length per shoot; (b) Mean leaf width per shoot, and (c) LAI. Bars represent ± 1 SE.

Annual means and ranges for environmental variables were: Surface irradiance, 1417 μmol photons m^{-2} s^{-1} (range of 331 to 2070); water temperature, 18.4°C (14.4 to 22.5); water salinity, 35.1‰ (33.0 to 36.9); nitrate, 1.5 μM (0.1 to 3.7); nitrite, 0.1 μM (0.01 to 0.3) and phosphate, 1.4 μM (0.7 to 4.6).

The PCA between leaf types and environmental variables indicated that each leaf type is related differently to physico-chemical variables: new leaves are positively correlated with phosphate, nitrite and water temperature; leaves shed are positively correlated with water salinity, and leaves present are positively correlated with water temperature and negatively with water salinity. Among leaves, the correlation between
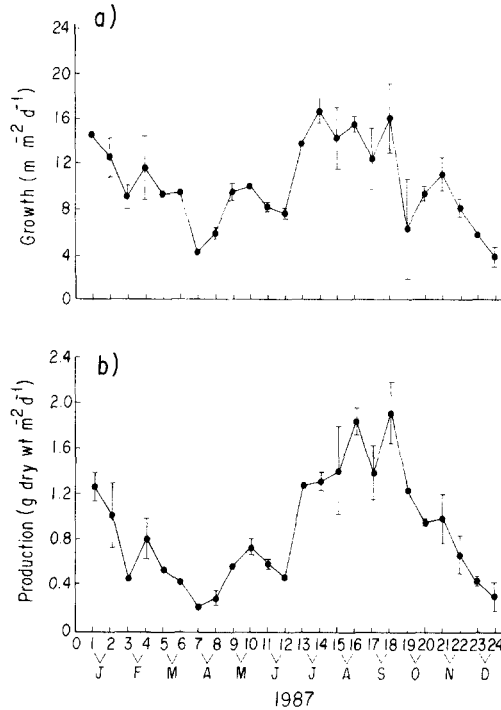
Fig. 3. Growth (a) and production (b). Data were standardized with shoot density information. Bars represent ± 1 SE.

new and present leaves was positive, and that between present and shed leaves was negative (Table 1). In this analysis, the first three axis explained 65% of the variance.

With respect to shoot morphometrics, no significant difference through time was found either for total length or average width ($P > 0.05$) (Fig. 2a and b). Annual means are 384 and 3.0 mm, respectively. The LAI did show significant differences through time ($P = 0.001$). Low values occur from February to June (average of 1.2 m^2 m^{-2}), while high values occur from July to October (3.6). The highest value was recorded in September (4.1) and the lowest in April (0.7). The annual mean is 2.3 m^2 m^{-2} (Fig. 2c).

Growth and production showed significant differences through time ($P = 0.03$ and 0.0001, respectively). Both graphs seem to follow the same pattern: Decreasing from the first half of January to the first half of April, then increasing from the end of April to the end of September (Fig. 3a and b). For growth, the lowest value was measured at the end of December (3.7 m m^{-2} d^{-1}), and the highest at the end of July (16.6). The annual mean is 10 m m^{-2} d^{-1} (Fig. 3a). In the case of production the lowest value is 0.21 g dry wt m^{-2} d^{-1} (end of April), the highest one is 1.9 (end of September), and 0.9 g dry wt m^{-2} d^{-1} represents the annual mean (Fig. 3b).

The relationship of growth and production with environmental variables, was investigated through a PCA in which the first three axis explained 73.6% of the variance. Growth is positively correlated with light and water temperature, and negatively

Table 2
Significant correlations between weighted growth, weighted production and environmental variables, obtained with a PCA

Variables	r	p
Growth		
Production	0.84	< 0.001
Light	0.48	< 0.02
Water temperature	0.42	< 0.05
Nitrate	−0.46	0.025
Phosphate	−0.42	0.04
Production		
Water temperature	0.68	< 0.001
Light	0.42	< 0.05
Nitrate	−0.43	< 0.05

correlated with nitrate and phosphate; production is also positively correlated with light and water temperature, and negatively correlated with nitrate. A positive correlation of 0.84 was found between growth and production (Table 2).

The plastochrone interval varied significantly through time ($P = 0.000$) and presents high values from January to April (mean value for this period, 10.2 days). An isolate
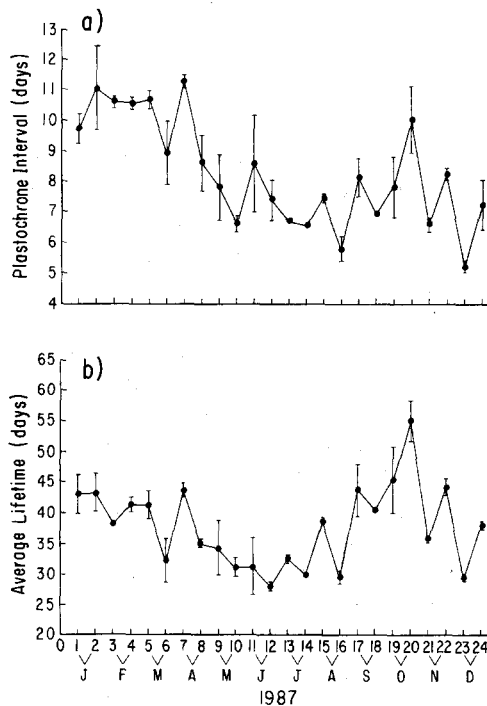

Fig. 4. (a) Plastochrone Interval and (b) average lifetime of a leaf in a shoot. Bars represent ± 1 SE.

high value of 10.0 was found during the second half of October. Low values correspond to the May–September period (mean of 6.9 days). The lowest (5.2) corresponds to the end of August (5.7 days), the highest one to the beginning of April (11.2 days), and the annual mean is 8.2 days (Fig. 4a). The average lifetime of a leaf over time had significant differences through time ($P = 0.002$). Low values correspond to the end of May–July and the end of August period (average of 30.3 days). High values are found during September, October and second half of November (average of 45.6 days). The lowest value is 27.8 days (end of June), the highest one is 54.9 days (end of October), and the annual mean is 37.6 days (Fig. 4b). The correlation between the plastochrone interval and the average lifetime of a leaf in a shoot is 0.61 ($P = 0.001$)

An annual mean for the turnover rate was calculated, yielding a value of 9.71 yr^{-1} (365 days/37.6 days), that means that during the year all the leaves in a shoot are renewed 9.7 times.

Two general observations apply to the measured variables: (1) low values are characteristic of the winter–spring period, and high values correspond to the summer–autumn period, and (2) initial and final values do not coincide and suggest interannual variations.

4. Discussion

The use of whole leaves allowed the identification of seasonal trends for most variables as well as significant correlations between them. These advantages have been previously discussed by Ibarra-Obando and Boudouresque (1994). Other authors had reported correlations between biological variables of the type: biomass–density (McRoy, 1970), leaf length–shoot density (Jacobs, 1979), leaf width–leaf weight (Nienhuis and de Bree, 1980), leaf surface area–shoot density (Kentula and McIntire, 1986), as predictors of eelgrass aboveground biomass. We were able to assess statistically the relationship between leaf types, between growth and production, and the one between plastochrone interval and average lifetime of a leaf in a shoot. We did not attempt to use any of these correlations as predictors, because the PCA was used only for exploratory purposes.

Our own data for leaf dynamics demonstrated that leaf presence and appearance are positively correlated, while leaf sloughing and leaf appearance are opposite but interdependent processes (when fewer leaves are sloughed, the number of leaves per shoot increases). This last result is in agreement with the findings of Sand-Jensen (1975) for *Z. marina*, and of Caye (1982) and of Wittman (1984) conclusions for *P. oceanica*. Leaves are constantly lost not only as part of the plant's life cycle but also as a result of environmental conditions. Some variables that have been related with seagrass leaf loss are grazers, currents and exposure to low temperatures and cold winds during winter (Zieman et al., 1979; Caye, 1982; Tomasko and Dawes, 1989). *Z. marina* grazers include ducks, geese and invertebrates (Nienhuis and van Ierland, 1978; Thayer et al., 1984; Nienhuis and Groenendijk, 1986). The effect of brant geese in Baja California's eelgrass beds has been documented by Kramer (1976) and Ward (1983).

The correlation between vegetative activity and environmental variables in *Z. marina* is not easy to determine (Phillips, 1976; Phillips et al., 1983). More recently, van Lent

and Verschuure (1994) mentioned that "direct statistical relationships between environmental factors and population dynamic characteristics could not be demonstrated, presumably because of interaction among environmental factors and intrinsic variability of populations". It is, however, known that environmental stability favors vegetative growth (den Hartog, 1970). This is why it was interesting to test whether this southern population, exposed to weak seasonal trends, would follow the annual pattern described for northern locations.

There is general agreement that light and temperature are the first two environmental variables that need to be considered when growth and production are evaluated (McRoy, 1970; Phillips, 1972; Sand-Jensen, 1975; Jacobs, 1979; Nienhuis and de Bree, 1980; Wium-Andersen and Borum, 1984; Kentula and McIntire, 1986; Sand-Jensen, 1989; van Lent and Verschuure, 1994). Our results and those of Solana-Arellano et al. (1977) for the same location are in agreement with these findings.

Total solar radiation and water temperature data for locations between 55° and 30°N, where perennial populations of *Z. marina* have been studied are presented in Table 3. The difference between water temperature minima and maxima for a given site fluctuates from 7°C (Jacobs, 1979; Phillips, 1972; our data) to 22°C (Wium-Andersen and Borum, 1980, 1984). With respect to solar radiation, differences go from 6 kcal cm^{-2} $month^{-1}$ (McRoy, 1966) to 13 (Wium-Andersen and Borum, 1980, 1984; Sand-Jensen, 1975; Kentula and McIntire, 1986; Bayer, 1979). Minimum variation in both water temperature and solar radiation corresponds to Puget Sound (Phillips, 1972) and San Quintin Bay (this study). No latitudinal trend can be identified (Table 3).

Information on leaf dimensions, dynamics and production of eelgrass populations at the above mentioned locations are summarized in Table 4. The studies included in the comparative analysis fulfilled the following criteria: they gave an annual year's cycle in the field, were a perennial population from the intertidal zone, and production was measured with a leaf marking technique. Nine papers were used, representing a latitudinal gradient from 56° to 45°N. Our data allowed a southerly extension to 30°N.

The comparison of San Quintin Bay data with those of northern latitudes indicates that the average number of leaves per shoot represents an intermediate value with respect to those previously reported; however, the small size of the leaves results in a maximum LAI of only 4.1 m^2 m^{-2}, that falls in the range of low values and is comparable only to Phillips (1972) data for Puget Sound, Washington. Growth and production are also low, but this result can also reflect technical differences. While all the marking techniques assess growth and production in leaf segments in the middle portion of leaves, the technique used during this study assesses the same variables in the basal portion of leaves, that weigh less. Meling-López (1995), working in San Quintin Bay, assessed *Z. marina* growth and production simultaneously with the technique of Kentula and McIntire (1986) and with the technique of Ibarra-Obando and Boudouresque (1994). Results demonstrated that during summer–fall the difference between techniques was significant (mean of 0.15 g dry wt $shoot^{-1}$ with Kentula and McIntire's technique, versus a mean of 0.08 with Ibarra-Obando and Boudouresque's technique), while no significant difference characterized the winter–spring period (mean of 0.04 g dry wt $shoot^{-1}$ for both techniques). The remaining variables in Table 4 give an indication of the high dynamic that characterizes our population, with the lowest values for both the

Table 3
Total solar radiation and water temperature data for different locations where perennial populations of *Zostera marina* have been studied. Solar radiation values were taken from Budyko (1963) and correspond to December and June respectively. Water temperature data correspond to minima and maxima reported by each author; in the case of Bayer (1979). where no temperature values were given. Netarts Bay values were used

Author	Site	Location		Solar radiation (kcal cm^{-2} month^{-1})	Water temperature (°c)
Wium-Andersen and Borum (1980, 1984)	Hvidøre (Denmark)	55.50° N	12.40° E	1 to 14	−2 to 20
Sand-Jensen (1975)	Vellerup Vig (Denmark)	55.52° N	11.49° E	1 to 14	5 to 22
McRoy (1966)	Izembek Lagoon (Alaska)	55.15° N	163.10° W	2 to 8	0.5 to 19
Nienhuis and de Bree (1980)	Lake Grevelingen (The Netherlands)	51.45° N	4.00° E	2 to 14	3 to 20
Jacobs (1979)	Roscoff (France)	48.44° N	3.59° W	2 to 14	9 to 16
Phillips (1972)	Puget Sound, WA (USA)	47.50° N	122.30° W	3 to 12	6 to 13
Kentula and McIntire (1986)	Netarts Bay, OR (USA)	45.26° N	123.56° W	3 to 16	4 to 25
Bayer (1979)	Yaquina Bay, OR (USA)	44.37° N	124.04° W	3 to 16	4 to 25
This study	San Quintin Bay (Mexico)	30.29° N	115.57° W	10 to 20	15 to 22

Table 4
Structural and functional variables reported for *Zostera marina* in shallow beds

Author	Average leaf length (cm)	Average Leaf width (mm)	LAI (m^2 m^{-2})	No. of leaves per shoot	Shoot growth (mm d^{-1})	Shoot production (g C m^{-2} a^{-1})	PI (days)	Lifetime (days)	Turnover rate (l a^{-1})
Wium-Andersen and Borum (1980)	NI	NI	0.4 (III)–7.6 (VIII)	3.6–6.1	0.8 (I to III)–48 (VIII)	266 (VIII–V)	14 (VIII & V)–120 (II)	NI	NI
Wium-Andersen and Borum (1984)	NI	NI	0.5 (IV) 7.7 (VIII)	3.7 (W)–6.1 (S)	1 (I) 58 (V)	554	9 to 14 (S)–60–120 (W)	NI	5.3 ?
Sand-Jensen (1975)	NI	NI	NI	3.0 (XI) 4.5 (VII)	20 (IV & X)–55 (VI)	328 (IV–X)	14	56	3.4
McRoy (1966)	29–68	1.7–2.9	NI	NI	NI	NI	NI	NI	NI
Nienhuis and de Bree (1980)	4.7 (III) 57 (VIII)	NI	NI	3.4	NI	207.5 (II to X)	14	48	6.4
Jacobs (1979)	23.8–59.8	NI	3.8 (III)–9.5 (VIII)	2.1 (XI)–4.4 (VI)	NI	389	13 (V) 28.7 (XII)	55–83	5.4
Phillips (1972)	17–60	1.5–4.5	1 (XII)–4 (IV)	4 (W)–5 (S)	NI	NI	NI	NI	NI
Kentula and McIntire (1986)	NI	NI	0.2–8.0	3.0–3.6	NI	383	7.0–25.6	27.4 55.5 (IV–IX)	9.8
Bayer (1979)	45 120	10.5–11.5	NI	NI	NI	NI	NI	NI	NI
This study	3.0–24	2.5 (IV)–3.7 (X)	0.7 (IV) 4.1 (IX)	2.9 (III)–5.1 (IX)	6.7 (IV)–20 (IX)	125 (I XII)	5.7 (VIII)–11.2 (IV)	29.5 (VIII)–43.6 (IV)	9.7

NI = Not Indicated. Roman numerals correspond to months. S = Summer; W = Winter

plastochrone interval, and average lifetime of a leaf in a shoot and the highest turnover rate (Table 4). The value of Kentula and McIntire (1986) for the turnover rate is the only one comparable to ours.

Our working hypothesis could not be accepted as, in general, our site follows the unimodal curve with maxima for each variable in summer and a minimum in winter as has been reported elsewhere (Nienhuis and de Bree, 1977; Jacobs, 1979, among others). With respect to seasonal behavior, Phillips (1972) mentions a summer (April to October) and a winter condition (November to March), and Thorne-Miller and Harlin (1984) identified an active growth period (April–November), and a winter period (December–March). In San Quintin Bay, winter and summer conditions, similar to those reported for Puget Sound could be recognized for most of the analyzed variables. With respect to leaf dimensions winter (small and narrow) and summer (long and wide) leaves have been reported elsewhere (Tutin, 1938; Burkholder and Doheney, 1968; Phillips, 1972; Kentula and McIntire, 1986). This seasonal difference in leaf dimensions could not be demonstrated during this study.

In conclusion, San Quintin Bay represents a favorable (stable) environment with respect to light and water temperature, allowing continuous eelgrass growth and production during the year. Two seasons are identifiable: Summer (May–October), when values increase and reach their maximum, and winter (November–April), when values tend to decrease. Maximum values in San Quintin were generally found in September, later than in more northern locations (Table 4). The intertidal zone is characterized by shoots of small dimension, whose growth and production values are low, but are very dynamic. We found evidence of interannual variations that require long term monitoring before they can be interpreted.

Acknowledgements

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