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# Annual variations of biomass and photosynthesis in *Zostera marina* at its southern end of distribution in the North Pacific

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## Abstract

Density, biomass, morphology, phenology and photosynthetic characteristics of *Zostera marina* were related to continuous measurements of in situ irradiance, attenuation coefficient and temperature at three coastal lagoons in Baja California, Mexico. In situ irradiance was approximately two-fold lower at San Quintin Bay (SQ) than at Ojo de Liebre Lagoon (OL) and San Ignacio Lagoon (SI). As a consequence of the greater irradiance, plants at OL and SI were established 1 m deeper within the water column than those at SQ. At SQ, there was a four-fold variation in biomass of *Z. marina* caused by changes on shoot length and not shoot density, while at OL and SI biomass and shoot length did not fluctuate significantly throughout the year. Reproductive shoot density reached maximum values concomitantly with the greatest irradiance during spring–summer, however, the density was approximately three-fold greater at SQ than at the southern coastal lagoons. While irradiance levels were two-fold greater at the southern lagoons, in general, photosynthetic characteristics were similar among all three lagoons. The hours of light saturated photosynthesis, calculated from their photosynthetic characteristics and irradiance measurements, suggest that photosynthesis of shoots from OL and SI are saturated for more than 6 h per day throughout the year, while shoots from SQ are likely light limited during approximately 15% of the year. Consequently, an increase in attenuation coefficient values in the water column will likely decrease light availability to *Z. marina* plants at SQ, potentially decreasing their survival.

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**Keywords:** Baja California; Hours of light saturated photosynthesis ( $H_{\text{sat}}$ ); Photosynthesis; Seasonality; Turbidity; *Zostera marina*

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## 1. Introduction

The distribution of seagrasses in coastal lagoons and estuaries is influenced by a variety of abiotic and biotic parameters, but light is generally considered the most important factor regulating their survival (Zimmerman et al., 1995; Koch and Beer, 1996). Depth distribution of *Zostera marina* L. (eelgrass) and other seagrasses, for example, is shallower in coastal lagoons and estuaries with greater turbidity than in clear water environments (Duarte, 1991; Olesen, 1996; Cabello-Pasini et al., 2002). Light reaching seagrass beds varies annually as a consequence of seasonal fluctuations in incident irradiance, daylength, water level, sediment resuspension, and organic matter concentration in the water column (McPherson and Miller, 1987; Zimmerman et al., 1994, 1995; Koch and Beer, 1996). Prolonged periods of light limitation, resulting from eutrophication or the resuspension of particulate matter, however, often leads to a decline of areas supporting seagrass growth or the mortality of deep growing plants (Zimmerman et al., 1995; Koch and Beer, 1996; Cabello-Pasini et al., 2002).

*Z. marina* (eelgrass) is the dominant submerged macrophyte in coastal lagoons of the Pacific coast of Baja California, Mexico (Ibarra-Obando and Rios, 1993). The Pacific coast of Baja California contains some of the largest beds of *Z. marina* in North America, and together with the Gulf of California represents the southern boundary of this species in the Northern Hemisphere (Riosmena-Rodriguez and Sanchez-Lizaso, 1996). *Z. marina* beds in Baja California are an important food source for tens of thousands of wintering waterfowl, including the majority of the brant (*Branta bernicla*) along the Pacific flyway (Reed et al., 1998), and form critical habitat for the recruitment of mollusks and fish (Santamaria et al., 1999). Over the last decade, the urban development of the coastal lagoons within Baja California as well as the establishment of shellfish aquaculture and salt mining has increased dramatically (Ortega and Castellanos, 1995). While the impact of these activities on the seagrass communities is unknown, a decrease in *Z. marina* abundance has been observed as a result of dredging operations in some coastal lagoons of Baja California (Cabello-Pasini, 1984).

Despite increasing threats to the coastal ecosystem of Baja California, there has been no comprehensive evaluation of the demography, phenology, and physiology of *Z. marina* across its distribution range in Mexico. Previous demography studies of *Z. marina* along the Pacific coast of Mexico have been confined largely to the northern coastal lagoons (30–32°N), Estero de Punta Banda and San Quintin Bay (SQ) (Cabello-Pasini, 1984; Ibarra-Obando and Huerta-Tamayo, 1987; Poumiant-Tapia and Ibarra-Obando, 1999), which lie within the central portion of the distribution range of *Z. marina* (Phillips, 1983). Similarly, studies in the Gulf of California have been localized to one population in Sonora (approximately 29°N) (Phillips, 1983; Meling-Lopez and Ibarra-Obando, 1999). While seasonal variations of eelgrass density and biomass in the northern lagoons have been suggested to be the result of annual fluctuations in water temperature, the effect of annual changes of in situ irradiance has not been assessed (Poumiant-Tapia and Ibarra-Obando, 1999). It has also been suggested that populations at the southern margin of the range of distribution are annuals, disappearing during the summer (Phillips, 1983). While this has been proven to be true for *Z. marina* populations at the Gulf of California (29°N), the life history, demography and physiology of populations growing further south (26°N) in the Pacific coast of the peninsula of Baja California are unknown. Consequently, the objective of this study was to characterize the annual variations in density, morphology, above-ground biomass,

flower density and photosynthesis of *Z. marina* populations at San Quintin Bay (30°N), Ojo de Liebre Lagoon (OL) (27°N) and San Ignacio Lagoon (SI) (26°N), in relationship to continuous measurements of in situ irradiance and temperature.

## 2. Materials and methods

### 2.1. Study site

The study was conducted at San Quintin Bay (30°25'N, 116°00'W; approximately 42 km<sup>2</sup>), Ojo de Liebre Lagoon (27°40'N, 114°05'W; approximately 500 km<sup>2</sup>) and San Ignacio Lagoon (26°55'N, 113°10'W; approximately 230 km<sup>2</sup>) along the Pacific coast of the peninsula of Baja California. San Quintin is one of the northernmost coastal lagoons in Baja California, and eelgrass populations at this site are considered within their central range of distribution in the Northern Hemisphere (Phillips, 1983). Populations of *Z. marina* at OL and SI, as well as populations from Magdalena Bay (25°N), represent the southernmost distribution of this species along the Pacific coast of Baja California. The peninsula of Baja California is an arid region and rainfall average is less than 11 cm per year with most occurring between October and March. There is little to no influx of surface water, but at SQ, adjacent dry river beds can fill with surface water runoff and drain to the bay during years of heavy rains (e.g. El Niño winters).

### 2.2. Environmental parameters

Air and seawater temperature, as well as incident and submarine photosynthetically active radiation (PAR) were recorded at 0.5 h intervals from January 1999 to April 2000 at each study site. Temperature was monitored using programmable thermistors (HOBO, Onset Computers, USA) calibrated in the laboratory against a digital thermometer. Air temperature was monitored from a protected weather station placed approximately 2 m above the ground while water temperature was monitored within the seagrass beds at approximately –1.0 m. Air and seawater temperature was averaged at daily intervals. Incident PAR and in situ irradiance levels were monitored using LI-190SA 2 $\pi$  quantum sensors (LI-COR) and LI-193SA 4 $\pi$  quantum sensors (LI-COR, USA), respectively. Underwater PAR sensors were placed at a height equivalent to the top of the *Z. marina* leaf canopy. Irradiance sensors were cleaned approximately every 2 months and the accumulation of small amounts of fouling between cleanings had no measurable effect on recorded values, as evaluated by the difference in irradiance immediately before and after cleaning. Incident and underwater irradiance was integrated daily from sunrise to sunset as mol quanta m<sup>-2</sup> per day. Scalar attenuation coefficient ( $K_0$ ) was calculated according to Beer's Law from incident and submarine irradiance values (Kirk, 1994).

Sediment grain size was determined in the *Z. marina* beds at SQ, OL and SI following the protocol described by Folk (1974). Sediment samples were collected every 50 m ( $n = 8$ ) to a depth of 7 cm using a 3 cm diameter core sampler. Samples were placed in 50 ml plastic tubes and transported to the laboratory in ice coolers. The sediment samples were placed in 400 ml beakers and cleaned from shells and debris. Samples were dehydrated in a 60 °C oven

until constant weight was obtained. Organic matter was oxidized using 35% (v/v) H<sub>2</sub>O<sub>2</sub> for approximately 1 week until no oxidation was evident and then samples were dehydrated in a 60 °C oven until constant weight was obtained. Approximately 30 g of sediment was placed at the top of a sieve stack (1–4.5  $\phi$ , 0.5  $\phi$  intervals) and sieved for 15 min in a Ro-Tap shaker. Sediments retained by each sieve were weighted in an electronic balance. Organic matter content in the sediment samples was obtained by difference in weight after oxidation with 35% (v/v) H<sub>2</sub>O<sub>2</sub> and dehydrating the samples to constant weight in a 60 °C oven as described previously.

The shore profile and depth of the seagrass beds was determined in two transects at SQ and one transect at OL and SI, respectively, using a transit, surveyor's rod marked every 1 cm and a metric tape. Transects were initiated at the highest tidal mark at each lagoon and ended at the deepest part of the *Z. marina* bed. Leveling marks were established at the nearest 0.5 cm. The depth of the eelgrass beds was adjusted to the mean lower low water (MLLW) level.

### 2.3. Shoot density and above-ground biomass

*Zostera marina* density was estimated approximately every 2 months from shoot counts using 400 cm<sup>2</sup> quadrats ( $n = 10$ ) at the three study sites. Quadrats were placed haphazardly throughout the middle of the *Z. marina* bed and shoots removed manually. Samples were placed in individual plastic bags inside ice coolers filled with seawater and transported to the laboratory for morphological and physiological measurements. In the laboratory, plants from each bag were separated and counted as vegetative and reproductive shoots. Dry weight (DW) from each bag was evaluated after drying the samples at 60 °C until constant weight was obtained.

### 2.4. Photosynthesis and respiration

Photosynthetic rates in leaves of *Z. marina* from SQ, OL and SI were determined using polarographically-measured rates of steady-state O<sub>2</sub> evolution (Rank Brothers, Inc., England). Approximately 0.1 g of tissue ( $n = 6$ ) from leaf #2 (youngest leaf = #1) was incubated in filtered seawater (0.45  $\mu$ m, pH 7.8, 2.1 mM DIC) at field temperature in 5 ml jacketed chambers connected to a water-circulating bath after a 0.5 h preincubation darkness. Halogen lamps (Quartzline, 300 W) were used as a light source, and photosynthetic photon flux (PPF) was varied using neutral-density filters (Lee Filters, England). Maximum oxygenic photosynthesis ( $P_{max}$ ), the initial slope of the photosynthesis versus irradiance curve ( $\alpha$ ), and the threshold for irradiance-saturated photosynthesis ( $E_k$ ) were determined by a non-linear direct fitting algorithm (Sigma Plot, Jandel Scientific) of the data to the exponential equation described by Webb et al. (1974). The hours of light saturated photosynthesis values ( $H_{sat}$ ) were calculated from the irradiance measurements and photosynthetic characteristics from *Z. marina* from all three lagoons according to Zimmerman et al. (1994) as:

$$H_{sat} = D \left[ 1 - \frac{2}{\pi} \sin^{-1} \left( \frac{E_k}{E_m} \right) \right] \quad (1)$$

Where  $D$  is the daylength,  $E_k$  is the threshold for irradiance-saturated photosynthesis and  $E_m$  is the irradiance value evaluated at solar noon.

## 2.5. Statistical analysis

Temporal and site differences in sediment grain size, shoot density and photosynthetic parameters were evaluated using a two-way ANOVA after testing for normality and homoscedasticity of the data (Sokal and Rohlf, 1981). Data were log transformed when assumptions for normality and homoscedasticity criteria were not met. Differences in organic content of the sediment among the three lagoons were evaluated using one-way ANOVA. All pairwise multiple comparisons were conducted using Tukey's test. The significance of correlations among environmental data, and between environmental data and demographic parameters were tested using Pearson's product moment correlations. Minimum significance level was established at  $P < 0.05$ .

## 3. Results

### 3.1. Environmental parameters

Sediment grain size in the *Z. marina* beds was bimodally distributed at SQ and unimodally distributed at OL and SI (Fig. 1). Grain size composition was relatively homogeneous at OL and SI where more than 90% of the sediment included fine and very fine sand, resulting in compact sandflats. In contrast, grain size composition was relatively heterogeneous at SQ, including approximately 20% silt and clays resulting in very soft substrate. Silt and clay composition was approximately 30-fold greater at SQ than at OL and SI. Organic matter comprised approximately 0.5% of the sediment dry weight at SQ and less than 0.1% at OL and SI.

As expected, air and water temperatures increased latitudinally from north to south (Fig. 2). Air and water temperature was lowest between December and March, and greatest between July and September at all three coastal lagoons. Maximum air temperature averaged approximately 22, 26 and 29 °C at SQ, OL and SI, respectively; however, temperature in the shade reached 40–48 °C during short periods in summer at OL and SI. Lowest temperatures averaged approximately 11, 13 and 15 °C at SQ, OL and SI, respectively. Maximum water temperature averaged approximately 22 °C at SQ and approximately 26 °C at OL and SI, respectively, while lowest water temperatures were similar (15 °C) at all lagoons. In general, there was a strong positive correlation ( $P < 0.05$ ) between daily averaged air and water temperature.

Daily-integrated irradiance followed a typical photosynthetic photon flux sinusoidal curve at all sites (Fig. 3). Although there was a clear seasonal irradiance signal, fog and clouds introduced considerable short-term variability into the incident irradiance. Maximum daily-integrated incident irradiance values were observed in June for all the three lagoons and increase from south to north. Maximum irradiance values were approximately 30, 55 and 62 mol quanta  $m^{-2}$  per day at SQ, OL and SI, respectively. Maximum irradiance was reached approximately 2 months before maximum air and water temperatures at all lagoons. Minimum daily-integrated irradiance values were approximately 5 mol quanta  $m^{-2}$  per day at SQ and approximately 25 mol quanta  $m^{-2}$  per day at OL and SI. Above-water and underwater daily irradiance were positively correlated ( $P < 0.05$ ) at all sites.

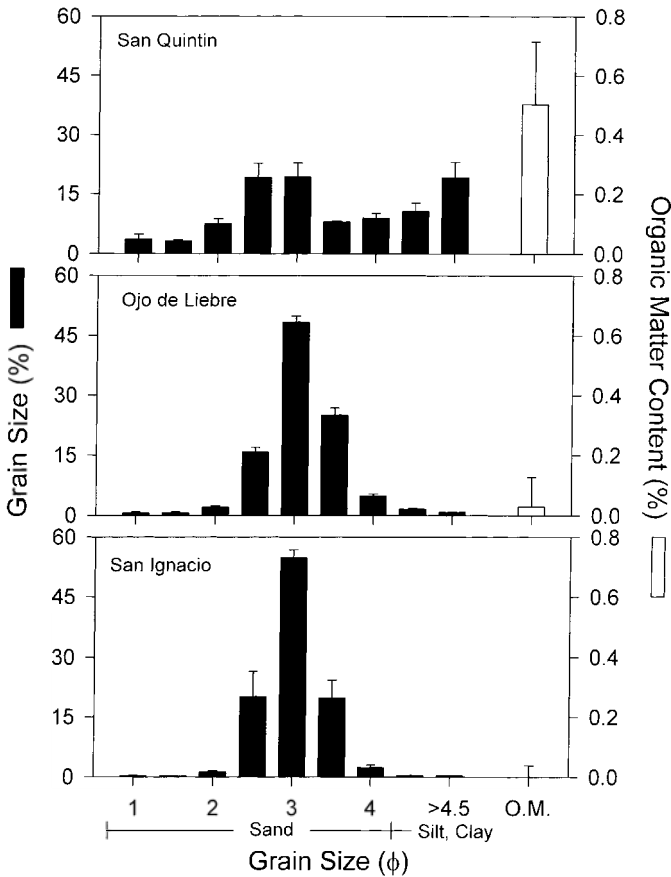


Fig. 1. Sediment grain size distribution (%;  $X \pm S.D.$ ,  $n = 8$ ) and organic matter content (%;  $X \pm S.D.$ ,  $n = 8$ ) within the *Z. marina* beds at San Quintin, Ojo de Liebre and San Ignacio.

Scalar attenuation coefficient values varied between the northern coastal lagoon and the two southern sites (Fig. 4). Values of  $K_0$  at SQ were approximately three-fold greater than those observed at OL and SI. At SQ, maximum values of  $K_0$  (approximately  $2.1 \text{ m}^{-1}$ ) were observed during the winter while minimum values ( $0.6 \text{ m}^{-1}$ ) were monitored during the summer. In contrast, maximum values of  $K_0$  (approximately  $0.5 \text{ m}^{-1}$ ) were observed during the summer while minimum values were determined during the winter ( $0.4 \text{ m}^{-1}$ ) at OL and SI. Transient periods of high  $K_0$  values were observed during the rainy season in winter at SQ.

### 3.2. Depth distribution, density, biomass and phenology

Distance from shore and depth of *Z. marina* beds varied among sites. The edge of eelgrass beds were located  $<250 \text{ m}$  from shore at SQ while edge of beds were  $>1200 \text{ m}$  away from shore at OL and SI. The upper limit of the depth distribution of *Z. marina* beds was approximately  $0.5 \text{ m}$  at SQ, while it is approximately  $-0.5 \text{ m}$  at OL and SI.

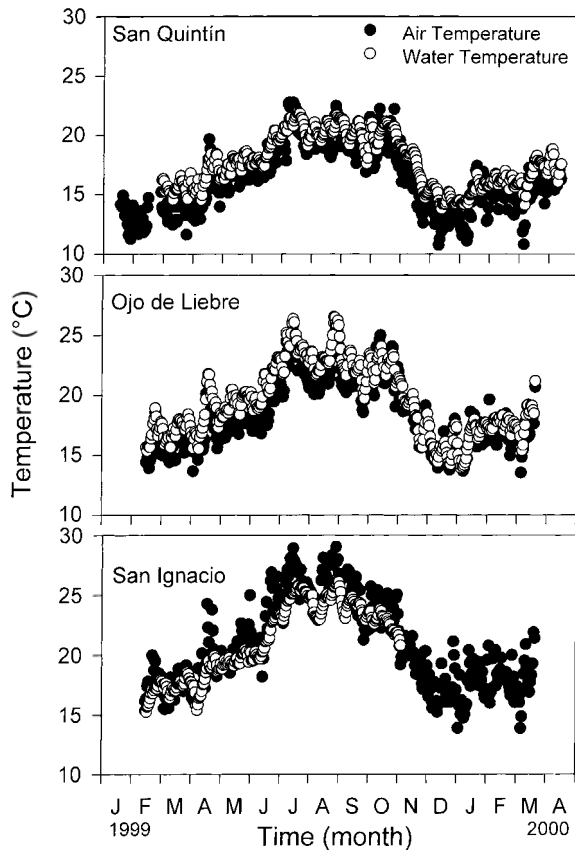


Fig. 2. Air and seawater temperature at San Quintín, Ojo de Liebre and San Ignacio throughout the study period. Temperature was recorded every 0.5 h using programmable thermistors and was averaged at daily intervals.

Annual average shoot density was significantly lower ( $P < 0.05$ ) at SQ ( $695 \pm 54$  shoots  $m^{-2}$ ) than at OL ( $992 \pm 50$  shoots  $m^{-2}$ ) and SI ( $1089 \pm 52$  shoots  $m^{-2}$ ). There was a significant effect ( $P < 0.05$ ) of time, site and the interaction term (time  $\times$  site) on the density of *Z. marina* (Table 1). Clear seasonal fluctuations of density over time, however, were only observed at SQ and OL (Fig. 5A). Maximum shoot density ( $1352 \pm 403$  shoots  $m^{-2}$ ,  $P < 0.05$ ) occurred during June at SQ and between June and September at OL ( $1457 \pm 158$  shoots  $m^{-2}$ ,  $P < 0.05$ ). Minimum shoot density occurred between October and February at SQ ( $501 \pm 77$  shoots  $m^{-2}$ ) and from February to March at OL (approximately 450 shoots  $m^{-2}$ ). In contrast to SQ and OL, shoot density at SI was relatively constant ( $1089 \pm 52$  shoots  $m^{-2}$ ).

Above-ground biomass showed a clear annual cycle at SQ and little but significant fluctuation at OL and SI (Fig. 5B, Table 1). Annual average biomass was approximately three-fold greater ( $P < 0.05$ ) at SQ ( $40 \pm 1.6$  gDW  $m^{-2}$ ) than at OL ( $8.9 \pm 1.5$  gDW  $m^{-2}$ ) and SI ( $13.7 \pm 1.5$  gDW  $m^{-2}$ ). At SQ, maximum biomass values ( $P < 0.05$ ) were detected in June

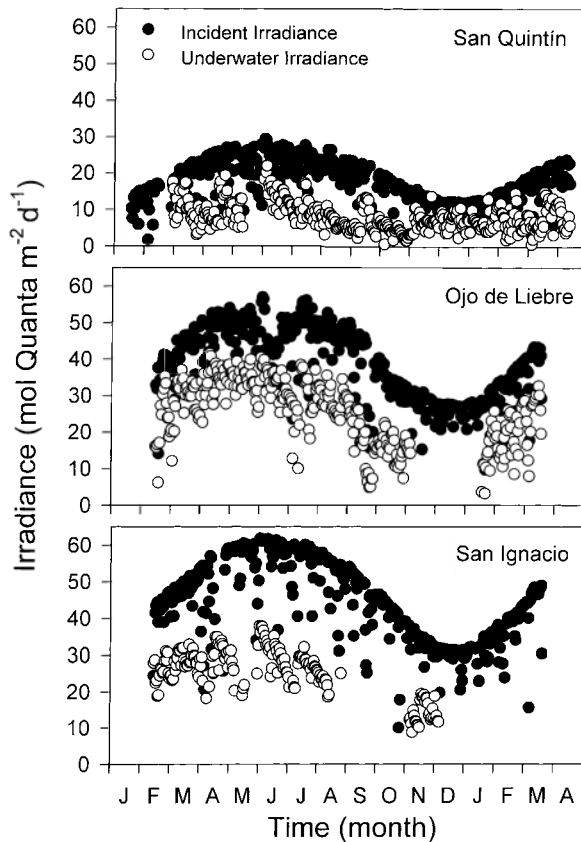


Fig. 3. Incident and underwater photosynthetic active radiation at San Quintín, Ojo de Liebre and San Ignacio. Irradiance levels were recorded at 0.5 h intervals throughout the study period and were integrated daily from sunrise to sunset as mol quanta  $\text{m}^{-2}$  per day.

( $236 \pm 68 \text{ gDW m}^{-2}$ ) while minimum values occurred in March 2000 ( $3 \pm 0.8 \text{ gDW m}^{-2}$ ). There was no strong seasonal pattern of above-ground biomass at OL and SI, though biomass levels were significantly higher in late summer than in winter.

The length of the *Z. marina* shoots increased significantly ( $P < 0.05$ ) between February and October at all sites (Fig. 5C). Average shoot length was approximately three-fold greater ( $P < 0.05$ ) at SQ ( $40.0 \pm 0.8 \text{ cm}$ ) than at OL ( $13.2 \pm 0.7 \text{ cm}$ ) and SI ( $12 \pm 0.7 \text{ cm}$ ). Shoot width was approximately two-fold greater ( $P < 0.05$ ) at SQ ( $0.54 \pm 0.01 \text{ cm}$ ) than at OL ( $0.26 \pm 0.01 \text{ cm}$ ) and SI ( $0.32 \pm 0.01 \text{ cm}$ ). Similarly, width of *Z. marina* shoots varied significantly ( $P < 0.05$ ) throughout the year (Table 1). Flowering shoot density also showed a clear seasonal pattern with maximum densities at the end of June at OL and SI and from June to July at SQ (Fig. 5D). During June, flowering shoots represented approximately 45% of total shoot density at SQ while flowering shoots accounted for only 10 and 25% at OL and SI, respectively. While there was a significant effect of time on the reproductive shoot density, no significant effect was observed on site and the interaction term (time  $\times$  site,

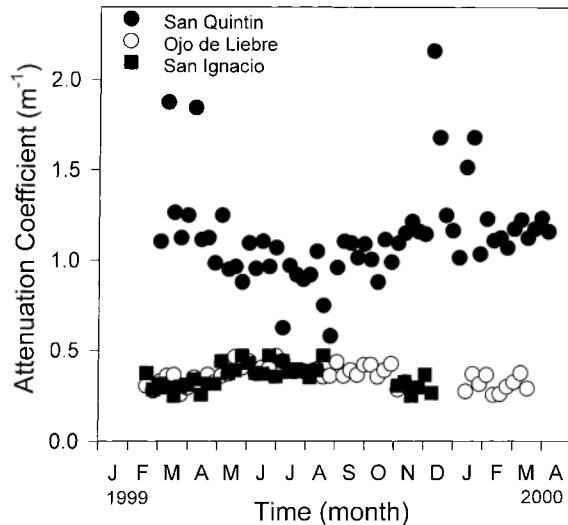


Fig. 4. Scalar attenuation coefficient ( $K_0$ ) at San Quintin, Ojo de Liebre and San Ignacio throughout the study period.

Table 1). Reproductive shoot density was positively correlated ( $P < 0.05$ ) to incident and submarine irradiance at SQ and SI.

### 3.3. Photosynthesis and respiration

The seasonal response of photosynthesis as a function of irradiance in *Z. marina* from all three study sites showed a typical exponential curve throughout the year (Fig. 6). There was a significant ( $P < 0.05$ ) effect of time, site and the interaction term (time  $\times$  site) on  $P_{\max}$  values of *Z. marina* at SQ, OL and SI, but values did not show a clear seasonal pattern (Fig. 7, Table 1). Bimonthly values of  $P_{\max}$  remained relatively constant over time, except during the winter of 1999 at all three lagoons. Similarly, there was a significant effect of time and the interaction term (time  $\times$  site) on  $\alpha$  of *Z. marina*, but there was no significant effect of site (Table 1). In general, values of  $\alpha$  showed a clear seasonal pattern at all lagoons with maximum values ( $P < 0.05$ ) observed during summer and lowest during winter. There was a significant effect of time, site and the interaction term (time  $\times$  site) on  $E_k$  values of *Z. marina* (Table 1). Values of  $E_k$  were relatively constant throughout the year at SI, while values decreased by approximately 50% at SQ and OL after the summer of 1999. There was a significant effect of time, site and the interaction term (time  $\times$  site) on the respiration of *Z. marina* (Table 1). Respiration values accounted for approximately 10% of maximum photosynthetic values in *Z. marina* from all three lagoons throughout the year, however, there was no clear seasonal respiratory pattern in *Z. marina* from SQ, OL and SI (data not shown).

There was a clear annual fluctuation of the hours of light saturated photosynthesis for *Z. marina* among lagoons (Fig. 8). Values of  $H_{\text{sat}}$  at all sites followed a sinusoidal pattern with maximum rates during June. Minimum  $H_{\text{sat}}$  values at SQ and OL were determined between November and January while minimum  $H_{\text{sat}}$  values could not be determined at SI.

Table 1

Results of two-way ANOVA testing the effects of time and study site on shoot density, biomass, shoot length, shoot width, flower density,  $P_{\max}$ ,  $\alpha$ ,  $E_k$  and respiration

Dependent variable	Independent variable	d.f.	MS	$F$	$P$	Significance
Density (shoots $m^{-2}$ )	Time	6	$1.5 \times 10^6$	8.5	<0.001	***
	Site	2	$2.5 \times 10^6$	14.6	<0.001	***
	Time $\times$ site	12	$1.3 \times 10^6$	7.5	<0.001	***
	Within	174	175183			
Biomass (gDW $m^{-2}$ )	Time	6	2268	14.7	<0.001	***
	Site	2	17107	110.9	<0.001	***
	Time $\times$ site	12	837	5.4	<0.001	***
	Within	174	154			
Shoot length (cm)	Time	6	4907	52.1	<0.001	***
	Site	2	41116	436.7	<0.001	***
	Time $\times$ site	12	1794	19.1	<0.001	***
	Within	856				
Shoot width (cm)	Time	6	0.26	47.9	<0.001	***
	Site	2	3.50	647.2	<0.001	***
	Time $\times$ site	12	0.03	7.14	<0.001	***
	Within	857				
Flower density (# $m^{-2}$ )	Time	5	1073	5.9	<0.001	***
	Site	2	508	2.8	0.065	n.s.
	Time $\times$ site	10	240	1.3	0.225	n.s.
	Within	112	181			
$P_{\max}$ ( $\mu\text{mol O}_2 \text{ gFW}^{-1} \text{ min}^{-1}$ )	Time	5	0.271	16.5	<0.001	***
	Site	2	0.115	6.9	0.002	**
	Time $\times$ site	10	0.064	3.9	<0.001	***
	Within	72	0.016			
$\alpha$ ( $\mu\text{mol O}_2 \text{ gFW}^{-1} \text{ min}^{-1}$ ) ( $-\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ ) $^{-1}$ )	Time	5	$5.6 \times 10^{-5}$	4.6	0.001	**
	Site	2	$2.5 \times 10^{-5}$	2.0	0.138	n.s.
	Time $\times$ site	10	$3.4 \times 10^{-5}$	2.7	0.006	***
	Within	72	$1.2 \times 10^{-5}$			
$E_k$ ( $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ )	Time	5	10752	4.2	0.002	**
	Site	2	13619	5.3	0.007	**
	Time $\times$ site	10	7473	2.9	0.004	**
	Within	72	2580			
Respiration ( $\mu\text{mol O}_2 \text{ gFW}^{-1} \text{ min}^{-1}$ )	Time	5	0.0081	7.96	<0.001	***
	Site	2	0.0058	5.75	0.005	**
	Time $\times$ site	10	0.0048	4.74	<0.001	***
	Within	72	0.0010			

No significance is indicated by n.s.

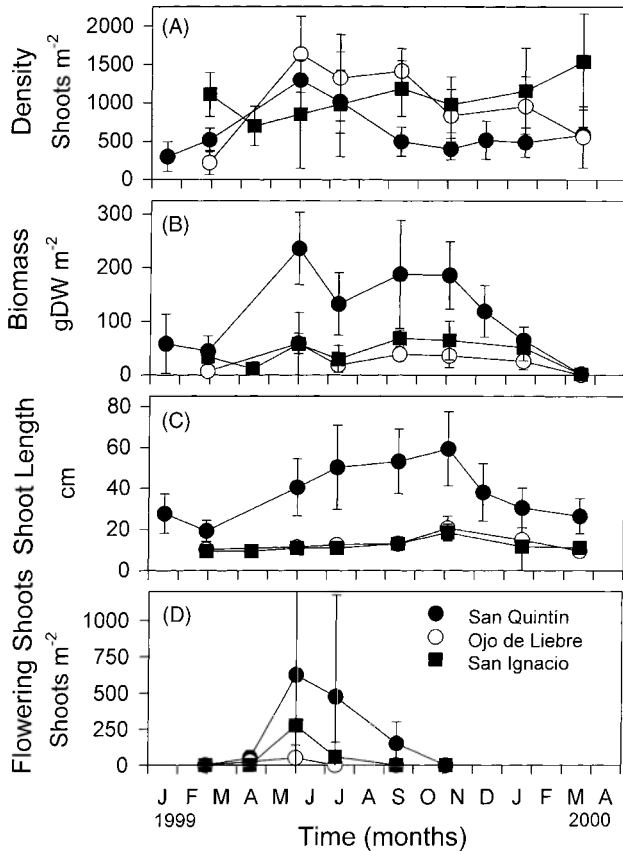


Fig. 5. Annual variation of: (A) density ( $\bar{X} \pm \text{S.D.}$ ,  $n = 10$ ), (B) biomass ( $\bar{X} \pm \text{S.D.}$ ,  $n = 10$ ), (C) shoot length ( $\bar{X} \pm \text{S.D.}$ ,  $n = 10$ ), and (D) density of flowering shoots ( $\bar{X} \pm \text{S.D.}$ ,  $n = 10$ ) of *Zostera marina* at San Quintin, Ojo de Liebre and San Ignacio throughout the study period.

There was greater  $H_{\text{sat}}$  fluctuation at SQ than at OL and SI, because of greater fluctuations of incident irradiance. While values of  $H_{\text{sat}}$  at OL and SI were greater than 8 h throughout the year, values were lower than 8 h approximately 62% of days at SQ. Furthermore, values of  $H_{\text{sat}}$  were 6 h or less for approximately 15% of the year at SQ.

## 4. Discussion

### 4.1. Environmental parameters and demography

Baja California encompasses temperate and tropical environments, and represents the southern limit of distribution for a number of land and marine organisms in the North-western Hemisphere (Riosmena-Rodriguez and Sanchez-Lizaso, 1996). This study reveals

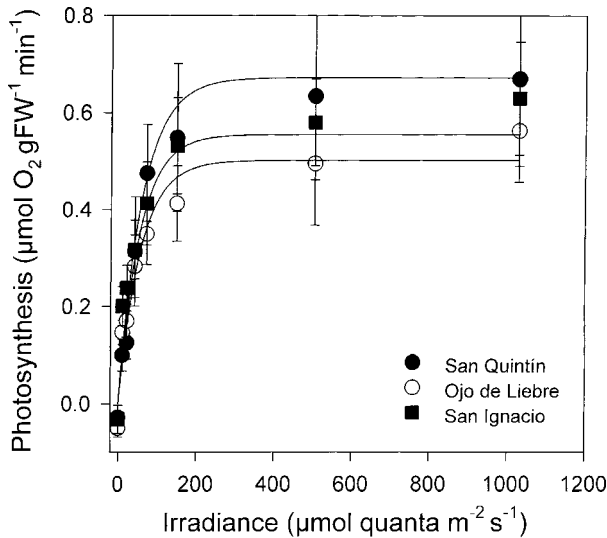


Fig. 6. Typical photosynthesis vs. irradiance response ( $\bar{X} \pm S.D.$ ,  $n = 6$ ) of *Zostera marina* shoots from San Quintin, Ojo de Liebre and San Ignacio evaluated polarographically. Error bars not shown are smaller than symbol size.

different temperature and irradiance conditions between a temperate coastal lagoon and two southern, more tropical, lagoons along the Pacific coast of Baja California. Our results suggest that such differences in environmental conditions have led to differences in morphological characteristics and depth distribution of *Z. marina* in this area. The photosynthetic response of the southern populations, however, is similar to those in populations from northern Baja California.

Evidence suggests that water transparency and light availability regulate the survival and depth distribution of seagrasses throughout the world (Zimmerman et al., 1995; Moore et al., 1997). Along with the lower incident irradiance levels, attenuation coefficient values were three-fold greater at SQ than at OL and SI resulting in less water transmittance at the northern coastal lagoon. The greater attenuation coefficient values observed at SQ are the result of the finer sediment content of this lagoon. Transient periods of high turbidity at SQ are probably the result of sediment resuspension and sediment input by wind from the agriculture fields adjacent to the lagoon, and wave action promoted by strong winds in the area and boat traffic in the lagoon. Furthermore, sediment loading from river flow during winter is likely a major factor in the transport of silts and clay into SQ Bay. In contrast to SQ, sediment at SI and OL is larger and settles faster in the water column promoting less turbidity, furthermore, rain and runoff of sediments from streams is negligible promoting clear water and high irradiance levels at the *Z. marina* canopies. Secchi disk depth also has decreased two-fold with the concomitant increase in oyster culturing and agriculture within and around San Quintin Bay in the last two decades (Alvarez-Borrego et al., 1977; Osorno-Velazquez, 2000). Along with the increase in water turbidity at SQ, there has been a decrease of abundance of subtidal meadows of *Z. marina* and a colonization of shallower intertidal mudflats (Ward et al., in review). Collectively, these data suggest that the lower

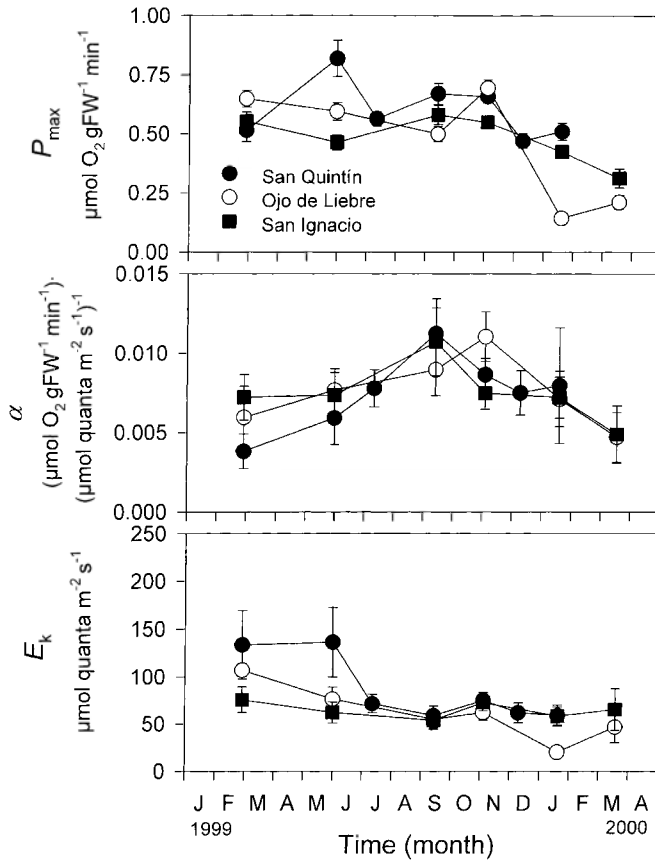


Fig. 7. Maximum photosynthesis ( $P_{max}$ ) ( $X \pm \text{S.D.}$ ,  $n = 6$ ), initial slope of photosynthesis vs. irradiance response ( $\alpha$ ) and light-saturated threshold for photosynthesis ( $E_k$ ) of *Zostera marina* at San Quintín, Ojo de Liebre and San Ignacio throughout the study period. Error bars not shown are smaller than symbol size.

incident irradiance and greater turbidity of the water have promoted the colonization of shallower areas at SQ than at OL and SI. Furthermore, the greater shoot length at SQ also suggests that plants are compensating for low light levels by elongating their leaves towards the surface of the water column.

Above-ground biomass of eelgrass in the field has been shown to be regulated by seasonal fluctuations of density and the number of leaves per shoot (Vermaat and Verhagen, 1996). In this study, the average density of *Z. marina* shoots as well as the number of leaves per shoot was relatively similar among all three lagoons throughout the year, however, shoot length and above-ground biomass was approximately four-fold greater at SQ than at OL and SI. There was also a much greater fluctuation of shoot biomass and leaf length at SQ than at the southern lagoons. This suggests that the greater annual fluctuation of above-ground biomass at SQ, relative to the southern lagoons, is the result of an increase in shoot area rather than shoot density fluctuations. This is inconsistent with findings by Vermaat and

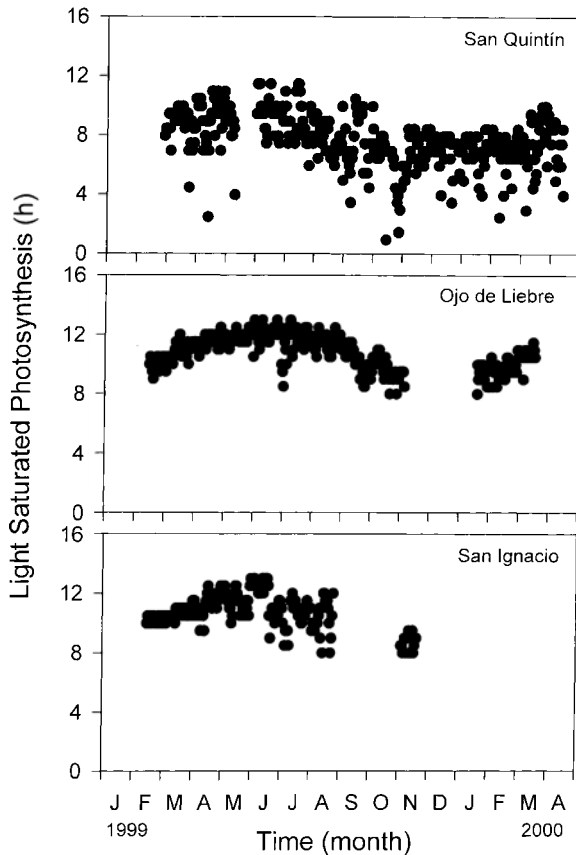


Fig. 8. Hours of light saturated photosynthesis ( $H_{sat}$ ) in *Zostera marina* from San Quintin, Ojo de Liebre and San Ignacio throughout the study period.

Verhagen (1996) where the variation in above-ground biomass was controlled by changes in shoot density and not shoot size. In contrast to plants at SQ, the little biomass fluctuation in the *Z. marina* beds from OL and SI is the result of the morphological uniformity of the shoots throughout the year. Similar to shoot biomass, below-ground biomass has been shown to be two- to three-fold greater at SQ than at OL and SI (Varela-Valencia, 2001). This suggests that there is an overall size reduction in plant size (root, rhizome and shoot) and biomass of *Z. marina* towards the southern end of distribution of this species.

The seasonal disappearance of annual populations of *Z. marina* at the southern end of distribution has been attributed to an increase in seawater temperature (Phillips, 1983; Meling-Lopez and Ibarra-Obando, 1999). Eelgrass populations in the Gulf of California (29°N) dieback during the summer months when water temperature surpasses 30 °C (Meling-Lopez and Ibarra-Obando, 1999). The seasonal persistence of *Z. marina* meadows at lower latitudes (SI, 26°N) in the Pacific coast of the peninsula, indicates that the annual life history is characteristic of only populations from the Gulf of California. Populations

from the Pacific coast of Baja California are not exposed to prolonged periods of water temperatures above 26 °C and consequently their life history resembles that of populations from the Pacific coast of the US and Canada.

Clear seasonal fluctuations in flower density are typical of seagrass populations worldwide, and appear to be driven primarily by light availability (Phillips, 1983; Vermaat and Verhagen, 1996). Consistent with those studies, flower production in the Pacific coast of Baja California increased during the period of maximum irradiance. The greater reproductive shoot density indicates a greater energy investment in seed production at SQ than at the southern coastal lagoons. In contrast to populations along the Pacific coast of Baja California, flower production in *Z. marina* beds in the Gulf of California appears to be regulated by water temperature (Meling-Lopez and Ibarra-Obando, 1999). While the annual water temperature fluctuation was greater at OL and SI, reproductive shoot density was greater at SQ, which further supports the hypothesis that flower density is regulated by light availability. Reproductive shoots accounted for a maximum of 45% of the vegetative tissue at the three lagoons, while at the end of the growth cycle in the Gulf of California, all shoots become reproductive and disappear after seed dispersal (Meling-Lopez and Ibarra-Obando, 1999; Santamaria et al., 2000). This indicates that the reproductive scheme of populations of *Z. marina* at the southern end of distribution in the Pacific coast is similar to those in the central region, and that the high rate of flowering shoot production is only characteristic of the annual populations from the Gulf of California.

While irradiance levels are two- to three-fold greater in Baja California, photosynthetic performance of *Z. marina* is lower than in populations from more northerly lagoons in California, USA (Zimmerman et al., 1994, 1995; Cabello-Pasini, 1996). This suggests that *Z. marina* at the southern end of distribution in Baja California is less productive than those from more temperate areas. Previous studies suggest that eelgrass requires up to 7 h of light saturated photosynthesis to maintain positive carbon balance and survive (Zimmerman et al., 1991, 1995; Alcoverro et al., 1999). Our data indicate that photosynthesis of *Z. marina* populations from OL and SI receive more than 8 h  $H_{\text{sat}}$  and is saturated throughout the year, however, plants at SQ can be light limited, especially during the winter months when  $H_{\text{sat}}$  values decrease to less than 4 h. Consequently, an increase in water turbidity in SQ, as observed in the last two decades (Alvarez-Borrego et al., 1977; Osorno-Velazquez, 2000), would most likely decrease the hours of light saturated photosynthesis in plants from this lagoon and threaten the survival of eelgrass, and possibly other submerged aquatic vegetation.

The photosynthetic performance of *Z. marina* was found to be similar among all populations studied despite the differences in water column turbidity and depth distribution. In contrast to the photosynthetic response, shoot chlorophyll levels were found to be two-fold greater at SQ than at the southern lagoons (Cabello-Pasini et al., 2003). This increase in chlorophyll levels is likely a physiological response of the shoots to the lower light availability at SQ, relative to the southern lagoons. The greater pigment level, as well as the greater leaf area, probably compensates for the lesser light availability at SQ and helps maintain a positive shoot carbon balance. Collectively, these data indicates that *Z. marina* is compensating for the reduction in light availability by modifying its morphological and biochemical characteristics.

Photosynthesis of *Z. marina* has been shown to decrease as a result of photoinhibitory processes caused by high irradiances (Aguirre-von-Wobeser, 2002). Consequently, it is

also possible that the colonization of deeper environments at OL and SI is a response to the high light environment at these lagoons and a mechanism to reduce photoinhibition of photosynthesis.

Roots and rhizomes generally account for most of the soluble carbohydrates in *Z. marina* and thus play an important role in the overall carbon balance. While photosynthetic ratios are similar among all lagoons, below-/above-ground biomass ratios are two- to three-fold greater at the southern lagoons than at SQ (Varela-Valencia, 2001). This suggests that the greater amount of hours of light saturated photosynthesis at the southern lagoons promote the generation of proportionally greater rhizomal systems to store photosynthates.

In contrast to populations from the Gulf of California, eelgrass beds at the southern end of distribution along the Pacific coast of Baja California appear to follow the typical demographic and reproductive schemes of more temperate populations. *Zostera marina* beds at SQ appear to be responding to low light availability, caused by high turbidity and low incident irradiance, by colonizing shallower environments. The southern *Z. marina* populations, however, are generally subtidal and appear to be less sensitive to annual fluctuations in irradiance and water temperature. In the last two decades, urban and industrial development has targeted coastal lagoons in Baja California and appears to have impacted the water quality in some of these fragile ecosystems. This study suggests that while eelgrass meadows at OL and SI have enough light to fulfill their carbon budget requirements throughout the year, an increase of the turbidity of the water column at SQ could decrease the survival of *Z. marina* and possibly other submerged aquatic vegetation.

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