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Seasonal variation in the biomass, size and reproduction of the agarophyte *Gracilariopsis sp.* (Gracilareaceae, Rhodophyta) from a temperate lagoon in the Pacific coast of Baja California Peninsula, México

Mario Antonio VERGARA-RODARTE[a], *Gustavo HERNÁNDEZ-CARMONA*[a*] *& Rafael RIOSMENA-RODRÍGUEZ*[†b]

[a]*Instituto Politécnico Nacional – Centro Interdisciplinario de Ciencias Marinas, Av. IPN s/n, Colonia Playa Palo de Santa Rita, La Paz, Baja California Sur, 23096, México*

[b]*Programa de Investigación en Botánica Marina, Departamento de Biología Marina Universidad Autónoma de Baja California Sur, Apdo. Postal 19-B, La Paz, Baja California Sur, 23080, Mexico*

Abstract – Spatial and temporal changes in the population structure and standing crop of *Gracilariopsis* sp. were studied in the San Ignacio Lagoon during two different sampling periods. Biomass (wet weight, g m^{-2}), thallus size and reproductive state were determined from November 2004 to August 2005. Standing crop was calculated from November 2007 to September 2008. The annual standing crop of *Gracilariopsis* sp. was estimated to be 1,300 wet tons. We found a seasonal growth cycle during both sampling periods, with the maximum biomass in spring (1,004 wet tons). Biomass was significantly higher near the mouth of the lagoon in shallow and sandy areas. This zone is associated with stronger currents and lower temperatures (annual mean of 20°C). The smallest thalli were found during autumn and winter, and the largest in spring. Senescence and detachment of the plants occurred in summer. Tetrasporangial thalli were the dominant phase in the population throughout the year, followed by vegetative (i.e. showing no reproductive structures) thalli. Gametophytes and carposporophytes were rarely observed during the study. The growth and propagation strategy of *Gracilariopsis* sp. in San Ignacio Lagoon is characteristic of a clonal population, which strongly suggests this species might be a good alternative for commercial agar production.

Growth Cycle / Biomass / Reproduction / *Gracilariopsis sp.* / Clonal

INTRODUCTION

Gracilariaceae are widely distributed from subarctic to tropical regions and are commercially important source of as raw material in agar production (Abbot, 1988; Armisen, 1995). Among the agarophytes, the genera *Gracilaria* and

* Corresponding author: gcarmona@ipn.mx
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Gracilariopsis are the major source of raw material for agar production worldwide (Levi *et al*., 1990). About 9,600 tons of agar (valued at US$ 173 million) were produced worldwide in 2009 and *Gracilaria* has become the preferred seaweed for the production of food grade agar. This is due to the success of its cultivation, the increase of availability and subsequent competitive prices (Bixler and Porse, 2011).

The Baja California Peninsula coast is the richest area of macroalgae in Mexico. There is a great abundance of alginophytes, agarophytes and carragenophytes (Cetz-Navarro *et al*., 2008). Twenty-two of the 38 species of Gracilariaceae and three of the seven species of *Gracilariopsis* reported for the Mexican littoral can be found along the coasts of the Baja California Peninsula (Dreckmann & Senties, 2014). *Gracilariopsis* sp. is the most abundant genus of macroalgae occurring in sandy-shallow areas within the San Ignacio Lagoon (Núñez-López & Casas-Valdez, 2000; Águila-Ramírez, 2003 as *Gracilaria pacifica*). This species was commercially harvested in the lagoon during the 1990's. Based on aerial surveys and commercial harvesting, the potential annual standing crop was estimated at 900 dried metric tons (Zertuche-González, 1993 as *Gracilaria pacifica*). Vergara-Rodarte *et al*. (2010) determined the seasonal variation in agar yield and quality. The highest alkaline agar yield was obtained in summer (17%) and the highest gel strength in spring (1,132 gcm^{-2}). The highest melting temperature was 98°C (winter) and the highest gelling temperature was 68°C (summer). They used the name *Gracilaria vermiculophylla* as result of the identification by Bellorin *et al.* (2004) from samples of *G. pacifica*. However, recent genetic evaluations suggest the material from San Ignacio Lagoon likely represents a species of the genus *Gracilariopsis* (Riosmena-Rodríguez, unpublished data).

Previous research in México focused on reinvigorating the harvest of this resource as an alternative fishery for local people. Temporal and spatial variation of *Gracilariopsis* sp. beds and how population parameters (size structure and reproductive condition) contribute to such variability is unknown. It is important to determine if the biomass of *Gracilariopsis* sp. is sufficient to sustain commercial exploitation for the agar industry, as previously suggested by Zertuche (1993). Studies of the reproductive structure of the population are also required to determine the natural recruitment of the species, because in natural populations it is common to find incomplete life cycles (Destombe *et al.*, 1989; Kain and Destombe 1995; Santelices, 2001). Changes in seaweed populations may also be related to particular environmental conditions (Lobban and Harrison, 1994). Water temperature, for example, is one of the main factors affecting the survival and growth of macroalgae (Lüning, 1990), therefore, temperature changes could influence macroalgal abundance and distribution.

The aims of this study were to: 1) describe the temporal and spatial variation in basic population parameters (biomass, size and reproduction) and 2) assess the potential seasonal harvest yield (standing crop) of *Gracilariopsis* sp. in San Ignacio Lagoon, Baja California Sur, México.

MATERIALS AND METHODS

The study was carried out in San Ignacio Lagoon (26º48'46''N 113º12'23''W), Baja California Sur, during two periods. In the first period (November 2004 to August 2005), we determined seasonal changes in basic population

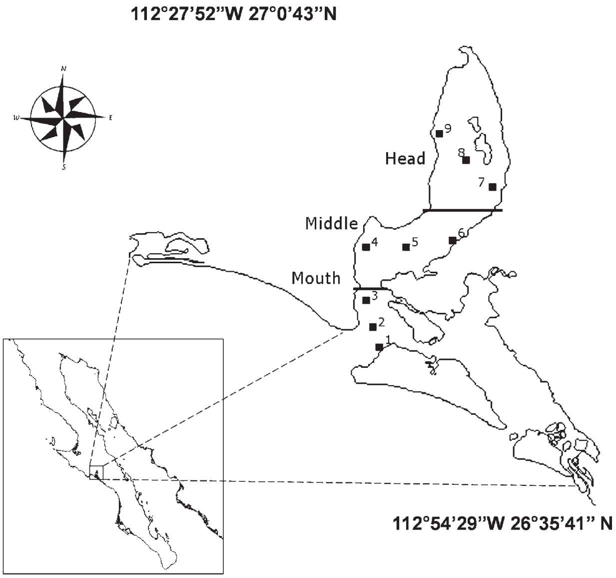

Fig. 1. The location of San Ignacio Lagoon in the central Baja California Peninsula, México.

parameters, including average biomass, reproductive stage, and size structure. The Lagoon was sampled in three zones: mouth, middle and head. Three sites were established in each zone based on previous observations of macroalgal distributions in the area. Two sites were located on the shallow side of each coast and one more in the middle of a channel at 5 m depth (Fig. 1). Sampling was carried out along a 50 m transect parallel to the coast at each site, and a 1 m^2 quadrat was placed every 10 m. All algae in the quadrats (n = 5 samples per transect and n = 15 per zone) were collected in mesh bags and excess water drained. The location of each sample was determined using a GPS. Samples were cleaned of associated fauna, seagrass and other seaweeds. The wet weight of *Gracilariopsis* sp. was determined using a balance. Samples were preserved in 4% formaldehyde in seawater. Additional monitoring was carried out along the coast using a boat and GPS to map the extent of *Gracilariopsis* sp. patches. Plant-size structure was calculated using each ramet from the samples obtained in years 2004-2005. Ramets were measured with a metric tape from the base to the longest ramification. Size frequency histograms were made using Sturge's formula (Daniel, 1996). To determine the reproductive condition of the beds, ramets were classified as vegetative (without reproductive structures) or reproductive (with reproductive structures). Each ramet was observed with a stereomicroscope (Olympus™). When the reproductive state of the ramet was unclear (sporangia, male or female gametangia or cystocarps), a cross-section was made and observed with an optical microscope equipped with an integrated camera (Olympus™) at 10× and 40× magnification. The number of vegetative ramets (VEG) and reproductive ramets was recorded, as well as the following structures: sporangium-tetraspore (ESP), cystocarp-female (CIS), and gametangia-male (GAM). Representative specimens were housed in the Phycological Herbarium of the Universidad Autónoma de Baja California Sur (FBCS 14500-14503), México. Specimens of *Gracilariopsis* sp. collected on February 20, 2011 were submitted for DNA sequencing to determine the species name (Riosmena-Rodríguez, unpublished data).

The data obtained from the sampling were tested for normality (Kolmogorov-Smirnov) and homoscedasticity (Bartlett) using the residuals from ANOVA analysis. Since data were neither normal nor homoscedastic, non-parametric statistics were done using the Statistical version 6 software. The Kruskal-Wallis test was used to determine significant differences in the wet weight of *Gracilariopsis* sp. among zones (mouth, middle and head). Since 99% of the biomass was concentrated in the mouth zone, only this area was used to assess seasonal variation of total biomass. The ratio of reproductive and vegetative ramets was assessed monthly for each site sampled at the mouth of the Lagoon. Kruskal-Wallis test was used to compare the reproductive stages per site and per month, using the median data (the middle value in the list of the data obtained).

The total biomass in the Lagoon was estimated during the second sampling period (November 2007 to September 2008). Sampling was carried out at the mouth of the lagoon and a new adjacent unexplored area called "Estero La Pitahaya". Sampling was carried out seasonally: autumn (November 2007), winter (February 2008), spring (May 2008) and summer (September 2008). The perimeter of each *Gracilariopsis* sp. bed was determined while traveling by boat and recording the coordinates every 5 to 10 m using a GPS (Lawrence, model: Finder-Explorer) until the perimeter was covered in the map. The area of each bed was assessed individually using MapInfo Professional version 8.0 software. Algal cover was assessed for each bed using a 1 m^2 quadrat with a 10 × 10 cm grid. The quadrat was placed every 10 m along two 50 m transects (n = 10 quadrats per bed) and percent cover was estimated based on the number of 10 × 10 cm squares covered by *Gracilariopsis* sp. Biomass was obtained by collecting all seaweed in ten 1 m^2 quadrats with 100% cover and these samples were drained and weighed. The total biomass present in each bed was calculated, multiplying the sampling biomass by the percent of area covered (Hernández-Carmona *et al.*, 1989).

Bottom water temperature was recorded every hour using an underwater hobo data logger (Onset Computer Corporation™) from November 2004 to August 2005 and from February 2007 to August 2008. An analysis of correlation between biomass and temperature was carried out using the data obtained. We also included other historical temperature data (1997-2003) to show that temperature during the study period was within the average of previous years, meaning that it was an average year (without ENSO effect).

Because of the complicated taxonomic history of the species a detailed histological analysis was carried out to determine the basic diagnostic features of the genera. Transverse sections of thalli were made to reveal the anatomical arrangement of the medulla, and the presence of male, tetrasporangial and carposporophyte conceptacles (Fig. 2).

RESULTS

Spatial and seasonal biomass variation

During the first study period (2004-2005), the population of *Gracilariopsis sp.* showed a clear spatial pattern, with significant differences between sampling zones ($p < 0.05$). The alga was found near the mouth of the lagoon, reaching a maximum biomass of 5 kg m^{-2}. In contrast, biomass in the middle and head zones

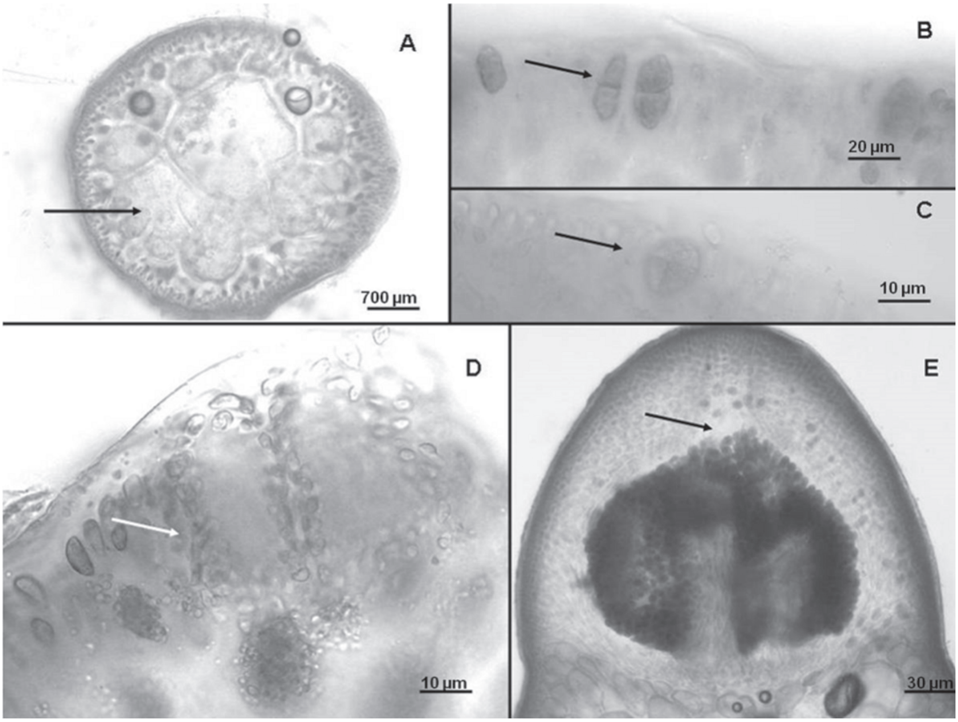

Fig. 2. Cross-section showing anatomical and reproductive characteristics relevant for identification. A) Cross-section of a ramet, showing the typical medullary cell arrangement of the genera. B) Cross-section showing a potential bisporangium in the epithelium. C) Cross-section showing a tetraspore. D) Cross-section showing a male gametangium. E) Cystocarp Cross-section showing carpospores and the lack of nutritive filaments.

was much lower with a maximum of 0.026 kg m^{-2} and the alga was absent in most of the quadrats. Based on this finding, only data obtained from the mouth zone are shown.

Seasonal variation in *Gracilariopsis* sp. biomass is shown in Fig. 3. *Gracilariopsis* sp. occurred in the lagoon throughout the year, with the lowest biomass in summer (400 g m^{-2}) and the highest in spring (1,245 g m^{-2}). *Gracilariopsis* sp. plants were smaller during autumn and winter and larger in spring. Larger size classes (80 cm, 100 cm and 120 cm), predominated in the spring (Fig. 4).

During the second sampling period (2007-2008), no *Gracilariopsis* sp. beds were found at the sites sampled in the previous period. Instead of *Gracilariopsis* sp., the substrate was occupied by beds of the seagrass *Zostera marina*. Thus, results are only reported for the Estero La Pitahaya and data for individual beds are summarized in Table 1. Despite this change, patterns in abundance were similar to the 2004-2005 study. The number of beds was variable because in some seasons algae were absent. Biomass varied significantly among seasons ($p < 0.05$). The maximum standing crop occurred during spring with 1,005 ± 424 wet tons (Fig. 3) in a total area of 32,7 hm^2. There was a significant decrease in biomass in summer, to 228 ± 52 wet tons ($p < 0.05$). Lower standing crops were found in autumn and winter.

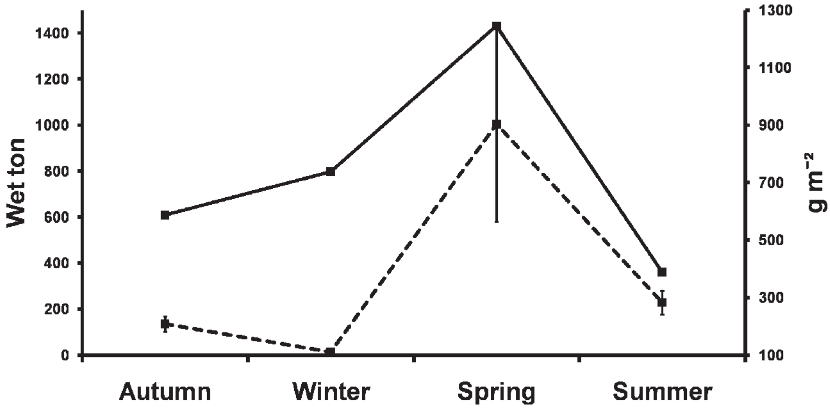

Fig. 3. Seasonal variation of biomass (g m^{-2}) for 2004-2005 (solid line, secondary axis) and total biomass (tons) during 2007-2008 (dashed line, main axis).

Table 1. Basic population parameters for the assessment of total biomass and location coordinates of *Gracilariopsis sp*. beds found in Estero La Pitahaya during 2007-2008. Bed number corresponds to the same bed in all seasons

	Bm *(kg m^{-2})*	At *(m^2)*	Cm *(%)*	*β*t *(ton)*	*SD (ton)*	*Latitude*	*Longitude*
				Autumn			
Bed 1	4.6	44,500	65	135	± 34	26’38.701”	113’7.59”
				Winter			
Bed 1	4.48	4,682	50	10.5	± 5.7	26’40.473”	113’7.103”
Bed 2	2.82	946	60	1.6	± 0.9	26’40.253”	113’7.274
				Spring			
Bed 1	1.25	2,500	50	1.5	± 0.75	26’41.431”	113’7.634”
Bed 2	5.92	2,100	65	8	± 3	26’41.387”	113’5.516”
Bed 3	5.35	104,700	60	336	± 106	26’41.257”	113’7.561”
Bed 4	2.26	80,700	40	73	± 45	26’41.056”	113’7.466”
Bed 5	2.26	600	90	1.2	± 0.75	***	***
Bed 6	11	50,000	75	414	± 209	26’38.902”	113’7.46”
Bed 7	11	1,500	40	6.6	± 3.1	***	***
Bed 8	5.26	21,000	70	83	± 15	26’40.121”	113’7.154”
Bed 9	2.24	60,000	55	74	± 38	26’40.369”	113.7.565”
Bed 10	2.24	3,750	85	7.1	± 3.7	***	***
				Summer			
Bed 1	5.5	21,880	85	102	± 17.5	26’40.627”	113’7.181”
Bed 2	5.5	450	60	1.5	± 0.25	***	***
Bed 3	5.5	9,170	60	30	± 5	26’40.810”	113’7.081”
Bed 4	5.2	15,900	83	70.5	± 22	26’40.605”	113’7.441”
Bed 5	5.2	15,300	30	24	± 7.5	26’40.815”	113’8.368”

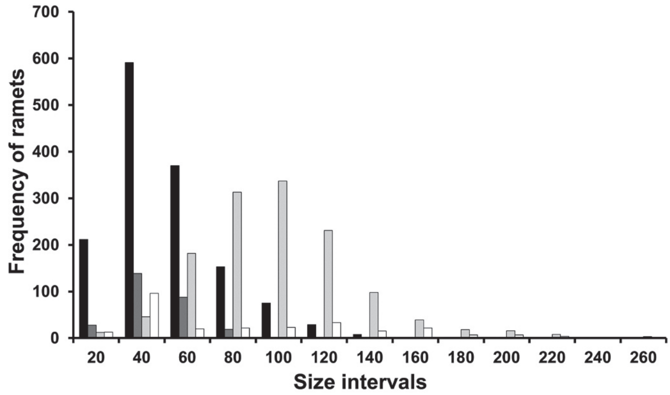

Fig. 4. Size class frequency structure of *Gracilaripsis sp.* (2004-2005). Autumn (black), winter (gray), spring (light gray), summer (white).

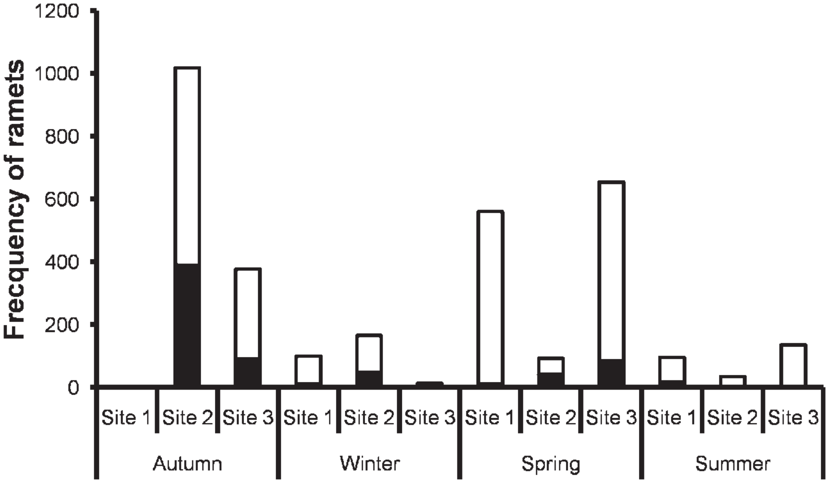

Fig. 5. Seasonal variation of vegetative (black) and reproductive-tetrasporic (white) ramets in the three study sites during 2004-2005.

Reproductive characteristics

The seasonal values obtained for the abundance of vegetative and reproductive (mostly tetrasporic) ramets of *Gracilariopsis* sp. during 2004-2005 are shown in Fig. 5. Over 3,000 ramets were examined and only one male thallus and two cystocarpic thalli were found. Most of the thalli observed were tetrasporic and vegetative. Tetrasporophytes were more abundant than vegetative thalli for all sites and seasons. The bottom seawater temperature at San Ignacio Lagoon was lower in winter (15ºC), then increased in spring to 20ºC, and was highest in summer, 27-28ºC (August-September) before decreasing in autumn to 17ºC (Fig. 6). There was a negative correlation between biomass (kg m^{-2}) and temperature ($r^2 = 0.887$, $p > 0.05$).

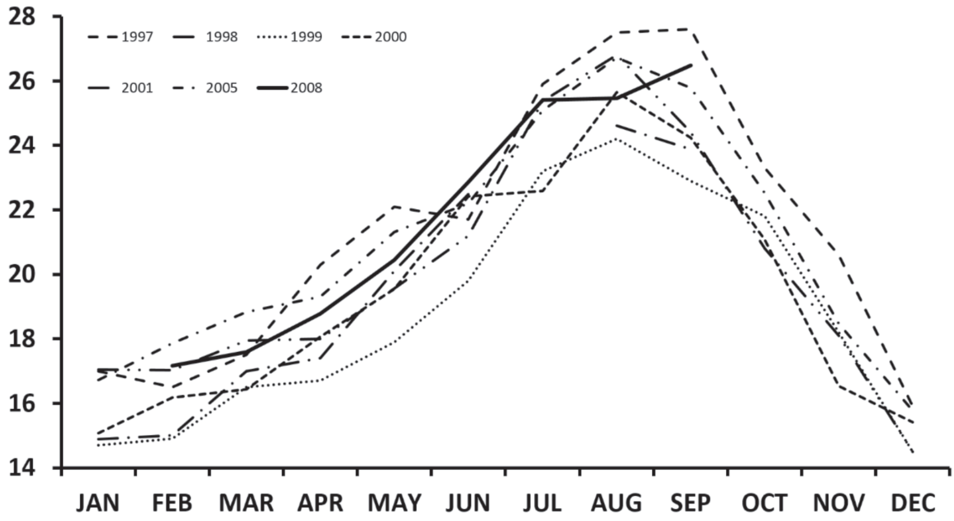

Fig. 6. Comparative monthly values of water temperature showing no significant variations in 11 years. Data provided by the oyster company Sol azul S.A de CV.

DISCUSSION

Gracilariopsis sp. beds were found mainly around the mouth of the lagoon in shallow and sandy areas, with stronger currents, and lower temperatures compared to the middle and head of the lagoon. The same spatial distribution was reported in previous studies in San Ignacio Lagoon (Núñez-López & Casas-Valdez, 1998; 2000), and for other Gracilaroid populations (Iknur & Cirik, 2004; Phooprong *et al*., 2007; Thomsen & McGlathery, 2007). Although we only measured water temperature, a combination of sandy bottom, low water temperature, strong currents, and high levels of irradiance may be the appropriate conditions for the development of this species. However, simultaneous measurements of each parameter and proper experimentation are required to test this hypothesis.

San Ignacio Lagoon is considered a temperate region, where cold water in winter and spring allows for an increase in seaweed abundance. *Gracilariopsis* sp. was present in the Lagoon throughout the year, but we found a clear seasonal fluctuation in total biomass and size structure. The maximum biomass and size occurred in spring, when reproductive thalli were also more abundant, coinciding with the maximum upwelling intensity caused by the California Current System, one of the world's most productive, which affects the western coast of the Baja California Peninsula (Zaytsev *et al*., 2003). This suggests that the maximum growth occurred in this season. Nevertheless, following the large abundance of *Gracilariopsis* sp. during spring, a senescence process began, which ended with plant detachment. After that, the seaweeds were deposited on the beach and practically disappeared during summer surveys. During this season, the water temperature exceeds 26°C, which is consistent with the negative correlation with biomass mentioned in the results. When the water temperature cools down in autumn and winter, growth begins, and the frequency of small-sized plants is increased greater. This same growth pattern was reported for other macroalgae on the eastern coast of the Baja California Peninsula, such as *Gracilariopsis lemaneiformis* (Pacheco-Ruíz *et al*., 1999), *Chondracanthus pectinatus* (Pacheco-Ruíz & Zertuche-González, 1999), and the alginophytes *Sargassum johnstonii, S. horridum* and *S. sinicola* (Pacheco-Ruíz *et al*., 1998; McCourt, 1984).

Additional observations during the study suggest competition for substrate occurred between *Gracilariopsis* sp. and *Zostera marina*. During the 2004-2005 sampling we observed *Gracilariopsis* sp. beds at the mouth of San Ignacio Lagoon, but in 2007-2008, the same beds were occupied by *Zostera marina*. Similar events have been reported between Gracilaroids and *Z. marina* in California (Huntington and Boyer 2008), and the Pacific coast of the Baja California Peninsula (Santamaría-Gallegos *et al*., 2001) and also with other seagrass *Ruppia maritima* (López-Calderón *et al*., 2010). In our case, this event only affected the spatial distribution of *Gracilariopsis* sp., because we found the same seasonal growth cycles in both study periods.

Reproductive characteristics vary considerably among Gracilaroids. For *Gracilariopsis* sp. in San Ignacio Lagoon, the population consisted of tetrasporic and vegetative plants, tetrasporophytes being more abundant throughout the year, whereas the carposporophyte and gametophyte phases were practically absent. This suggests that the triphasic growth cycle of this species is not complete in this area. A similar situation was reported for other Gracilaroids (Rao, 1973; Santelices & Ugarte, 1990; Aguilar-Rosas *et al*., 1993). The presence of one of the different propagation mechanisms (carpospores, tretraspores and vegetative fragmentation from diploid or haploid plants) might depend on environmental conditions, plant density, water velocity, salinity, temperature, geographic distribution, type of substrate and spore survival under these conditions (Destombe *et al.,* 1989; Aguilar-Rosas *et al.,* 1993; Guillemin *et al*., 2008). It has even been reported that some populations only use vegetative fragmentation as a propagation mechanism (Molloy & Bolton, 1995; Smith *et al.,* 2004).

Sexual reproduction and carposporophyte formation were not present for *Gracilariopsis* sp., and the combination of a high current and sandy bottom, create abrasive conditions that interfere with spore attachment. In summer, when fragmentation begins, the fragments are extensively washed away to the beach, suggesting that the attachment of new thalli by fragmentation is extremely unlikely. It was documented that the longevity pattern of Gracilaroids, including *Gracilariopsis* sp. is perennial, which implies that at least some part of the thallus is present throughout the year (Mathieson, 1989), probably the underground thallus system. In some Gracilaroid species, this part of the thallus must have the ability to survive long periods of burial (Santelices *et al.,* 1984). Some authors have suggested that this system might be the most important mechanism for the regeneration and propagation of some Gracilaroid populations (Santelices *et al.,* 1984; Santelices, 2001). This growth and propagation ability of *Gracilariopsis* sp. in San Ignacio Lagoon suggests that it forms a clonal population, according to the definition of Santelices (2001). For commercial purposes, this type of population is more suitable than one based on sexual reproduction, because the development of reproductive structures represents an energy cost, which affects the growth rate and quality of the phycocolloids (Santelices &Varela 1995; Givernaud *et al.,* 1999; Marinho-Soriano *et al.,* 1999; Marinho-Soriano & Bourret, 2005).

Despite the significant differences in biomass among seasons, there is harvest potential for this alga, which would promote seasonal jobs for fishermen as part of local programs. Previous studies have demonstrated the economic importance of this alga (previously reported as *Gracilaria vermiculophylla*), which can be used as a raw material for agar production (Vergara-Rodarte *et al.,* 2010). The agar produced from this alga has a higher gel strength after alkaline treatment (900-1,100 g cm^{-2}). The duration of this alkaline treatment is reduced relative to those used in production of commercial-grade agar from other species, making it more economically suitable. A better understanding of the biology of this species would lead to the implementation of large-scale cultures and therefore greater benefits.

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