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Recruitment in *Ulva* blooms in relation to temperature, salinity and nutrients in a subtropical bay of the Gulf of California

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Abstract: *Ulva* blooms are highly productive ephemeral communities that occur in coastal systems, associated with nutrient enrichment. The objective was to estimate variations in succession, cover, recruitment and length of *Ulva* species in four blooms and assess their relationship with environmental parameters in Bahía de La Paz, Baja California Sur. At each locality, monthly samplings were performed to register the presence, recruitment, length and cover of species, and temperature, salinity, turbidity and nutrient concentration in surface seawater from February 2013 to October 2015. The species found were *Ulva acanthophora, Ulva clathratha, Ulva intestinalis, Ulva flexuosa, Ulva lactuca, Ulva lobata, Ulva nematoidea* and *Ulva rigida*. The *Ulva* blooms in Casa del Marino, San Juan de la Costa and El Tecolote were multi-species, with *U. rigida* displaying the highest presence, cover and recruitment, followed by *U. acanthophora*. Significant differences were found between localities, years and months for biological and environmental factors. A principal component analysis (PCA) revealed significant relationships between higher cover, recruitment and length with higher nutrients concentrations at San Juan de La Costa, Casa del Marino and El Tecolote, indicating favourable conditions that allowed rapid growth. The cover, recruitment and length of *U. flexuosa* at El Portugués were inversely correlated with temperature.

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Introduction

Macroalgal blooms in coastal waters are increasingly common and recurrent. These communities are ephemeral, highly productive, and are formed by the rapid growth and reproduction of the algae, and the increase in the abundance of one or more species of opportunistic macroalgae. These species are characterised by high photosynthetic, growth and nutrient uptake rates (Lotze and Shramm 2000).

The blooms of green algae such as *Chaetomorpha*, *Cladophora, Ulvaria* and *Ulva* produce “green tides” associated with nutrient rich waters from river runoff, upwelling events or discharge of untreated domestic and/or industrial sewage (Zhao et al. 2013).

Recruitment and biomass of *Ulva* increases by one to two orders of magnitude when nutrient enrichment coincides with optimal temperatures. Physiological traits of ephemeral macroalgae enhance their success when there is a successional process, as a result of an increment in nutrient loads, in which the vegetation is initially dominated by species that display the highest reproduction rates, characterised by simple thalli and little biomass (Lotze and Shramm 2000).

Some studies on the biomass of *Ulva* have been performed in localities of the Gulf of California (Pacheco-Ruíz et al. 2002). Macroalgal communities have been assessed at the Bahía de La Paz, and the abundance of *Ulva* has been evaluated in La Paz boardwalk (Águila-Ramírez et al. 2005). However, the recruitment and succession of *Ulva* blooms have not yet been described, nor the relationship with hydrographic, environmental and nutrient-related parameters in the Gulf of California.

This genus displays rapid growth rates, a wide range of reproductive strategies and a fast response to increased concentrations of growth limiting nutrients that lead to a significant increase in biomass (Sousa et al. 2007). The objectives of the present work were to determine the patterns of succession, cover, recruitment and length of *Ulva* species on algal blooms in a subtropical bay, as well as their relationship with hydrographic parameters and nutrients.

Materials and methods

Study area

Bahía de La Paz is a semi-protected water body located on the Gulf of California's western coast. This study was conducted in four sampling localities where blooms of *Ulva* species occur (Figure 1): El Portugués (the beach consists of a mix of boulders and sandy patches), San Juan de la Costa (sandy bottom and boulders), Casa del Marino (protected shallow area of sandy bottoms with some boulders, shells and coral remains) and El Tecolote (long rocky platform).

Environmental variables

In each locality, during low tide, surface seawater temperature (SST), salinity and turbidity of the water column were measured monthly using a multi-parameter probe (Horiba U-50, Horiba, Ltd., Kyoto, Japan). Three water samples were collected from the surface of the water column using 1-l bottles previously washed with deionised water. These samples were placed on ice for transport to the laboratory for subsequent analysis; the concentrations of dissolved inorganic nitrogen (DIN), total nitrogen (TN), orthophosphates (PO_4) and total phosphorus (TP) were determined using the techniques described in Strickland and Parsons (1972).

Succession, cover and length

In each locality, monthly visits were carried out from February 2013 to October 2015. The area of each algal bloom was measured with GPS (Garmin, Ltd., Olathe, Kansas, USA) and the limits were marked in the shore for future reference. To determine the changes in succession and plant cover by species, eight permanent 0.50 × 0.50 m quadrats built with PVC pipe (1.27 cm Ø) were positioned haphazardly in each bloom area. At the beginning of the study, all the algae and other organisms inside each quadrat were removed by scraping with a spatula and a metal wire brush. The species present and the percent cover of each were recorded each month through photographs (Yáñez-Chávez et al. 2008), which were analysed with the software Coral Point Count with Excel extensions

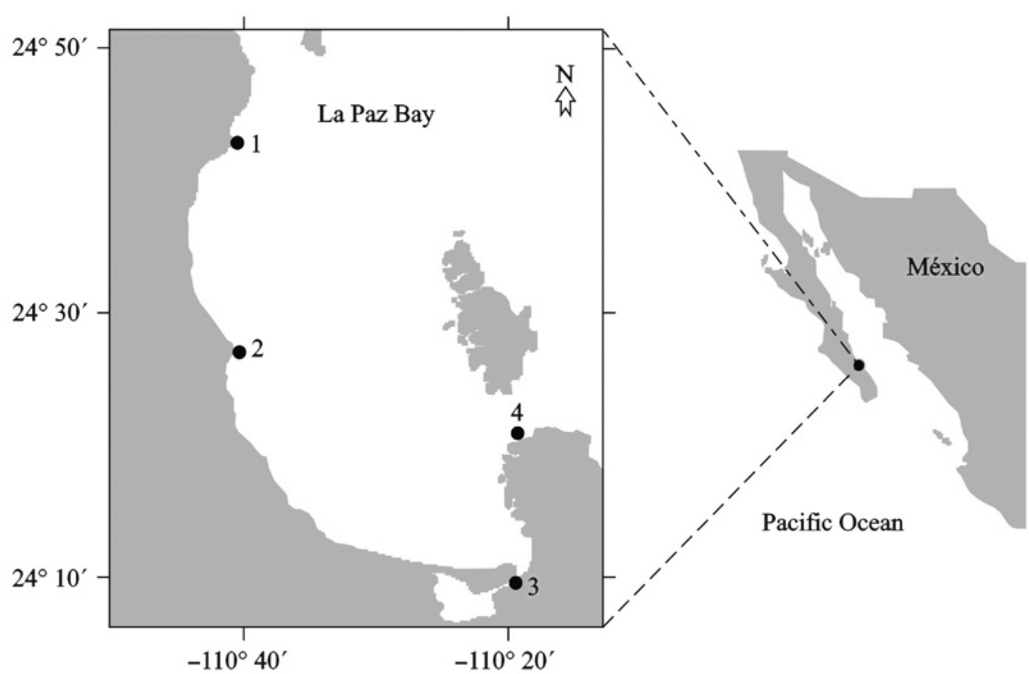

Figure 1: Location of study area of *Ulva* species.
(1) El Portugués, (2) San Juan de La Costa, (3) Casa del Marino and (4) El Tecolote.

(National Coral Reef Institute's, Nova Southeastern University Oceanographic Center, Ft. Lauderdale, FL, USA). In these quadrats, the length of 10 haphazardly chosen thalli (larger than 0.1 cm) of each species of *Ulva* was measured each month.

Recruitment

A further eight permanent 0.50 × 0.50 m quadrats were positioned haphazardly in each bloom area, ensuring no overlap with the quadrats used for estimating plant cover. All the algae and other organisms in each quadrat were removed initially, and all recruits within this area were collected each month, leaving the substrate clean again. Recruits were placed on ice for transport to the laboratory, where they were sorted by species and then weighed (wet weight). A sample was taken from each morphotype collected and fixed in 4% formaldehyde for identification using the appropriate keys for this genus in the Gulf of California, which are based on external and internal morphological characters (Abbott and Hollenberg 1992, Norris 2010). Based on these characteristics, the nearest species name was assigned for each morphotype collected. Completely reliable identification of species of this genus is possible only by means of molecular analysis, which was not available for this study, but is recommended when working with this genus.

Data analysis

Before each statistical analysis was run, Kolmogorov-Smirnov and Levene's tests were performed to check dataset normality and homoscedasticity, respectively (Zar 2010). Means and standard errors (SE) were calculated. To test for significant annual, monthly and spatial differences in cover, recruitment and length of *Ulva*, as well as in temperature, salinity, turbidity and concentration of nutrients in the water column, a multivariate analysis of variance (MANOVA) ($p < 0.05$) and *post-hoc* comparisons using Tukey's test ($p < 0.05$) were performed (Zar 2010).

The relationships between biological variables and environmental parameters were explored through a principal component analysis (PCA). In the numerical analysis, the significance criterion for each component (factor) is the intrinsic proper value of that factor (eigenvalue), i.e. if this value is >0.1 the factor is deemed significant (Santa María-Del Ángel et al. 1992). The greatest absolute values obtained from the correlation matrix were used to explain the relationships within the plane of each factor, values with the same sign indicating a positive correlation, and different signs an inverse association. The analyses were performed with the software STATISTICA 7.1 (Statistica, Tulsa, OK, USA) (StatSoft Inc. 2013).

Results

Environmental parameters

There were highly significant variations in the mean values of SST, salinity, turbidity and nutrients among the four sites, over the 3 years and from month to month, and these variations and most two- and three-way interaction effects were significant (Table 1). The exceptions were: the interaction between site and year did not affect salinity or DIN, the interaction among site, year and month did not affect PO_4, and both DIN and TN did not vary significantly among the years (Table 1).

The highest values of SST were found from August to October 2014, and June to October in 2015 for the four localities (Figure 2A). The lowest values were found at El Tecolote during February 2013 and 2015 ($p < 0.05$). In general, salinity values varied little (Figure 2B); however, the highest values were found at Casa del Marino during February, May, June and December 2013 and April, May, June and August 2014. Lower values were found at El Portugués, particularly during 2013 and at El Tecolote only during November 2013 ($p < 0.05$). Turbidity showed a broad variation across time and localities (Table 1) with no distinguishable pattern.

DIN values at San Juan de la Costa during September and October 2014 were five times higher than the rest of the months and localities (Figure 3A); however, in April, May, July 2013, July and August 2014 at San Juan de La Costa and January 2015 at San Juan de La Costa and Casa del Marino, values were also higher than in the rest of localities and months ($p < 0.05$). Peaks in TN (Figure 3B) were found during August, September and October 2014 at El Tecolote and San Juan de la Costa and during May 2015 at El Portugués, and were almost three-fold higher than those found at the same localities during November 2014 and March, June and August 2015 ($p < 0.05$).

For PO_4 (Figure 3C), the highest values were found at San Juan de la Costa during March 2014 and January and March 2015, and were three times higher than the values found at the same locality during June 2013 and May, September and October 2014 and at Casa del Marino during May and July 2014 ($p < 0.05$). For TP (Figure 3D), the highest values were found at San Juan de la Costa during September and October 2015, and these values were four times

Table 1: Results of MANOVA on surface seawater temperature (SST), salinity, turbidity, dissolved inorganic nitrogen (DIN), total nitrogen (TN), orthophosphate (PO_4), total phosphorus (TP) among site, year, month and their interactions.

Factor	Interaction	df	MS	F	p-Value
Temperature	Site	3	37.1	57.0	**<0.0001**
	Year	2	173.6	266.6	**<0.0001**
	Month	11	251.1	385.6	**<0.0001**
	Site*Year	6	5.3	8.1	**<0.0001**
	Site*Month	33	5.4	8.3	**<0.0001**
	Year*Month	19	15.6	24.0	**<0.0001**
	Site*Year*Month	57	4.3	6.7	**<0.0001**
	Error	357	0.7		
Salinity	Site	3	13.0	26	**<0.0001**
	Year	2	7.8	16	**<0.0001**
	Month	11	6.9	14	**<0.0001**
	Site*Year	6	1.1	2	**0.0417**
	Site*Month	33	1.5	3	**<0.0001**
	Year*Month	19	2.0	4	**<0.0001**
	Site*Year*Month	57	1.7	3	**<0.0001**
	Error	357	0.5		
Turbidity	Site	3	389.70	7.1208	**0.0001**
	Year	2	715.04	13.0656	**<0.0001**
	Month	11	466.06	8.5161	**<0.0001**
	Site*Year	6	933.90	17.0647	**<0.0001**
	Site*Month	33	286.35	5.2324	**<0.0001**
	Year*Month	19	235.53	4.3038	**<0.0001**
	Site*Year*Month	57	207.62	3.7938	**<0.0001**
	Error	357	54.73		
DIN	Site	3	10972.86	105.3160	**<0.0001**
	Year	2	43.43	0.4168	0.6597
	Month	11	776.91	7.4566	**<0.0001**
	Site*Year	6	165.66	1.5900	0.1514
	Site*Month	33	884.71	8.4913	**<0.0001**
	Year*Month	19	439.67	4.2199	**<0.0001**
	Site*Year*Month	56	546.35	5.2438	**<0.0001**
	Error	207	104.19		
TN	TN				
	Site	3	10928.5	27.0859	**<0.0001**
	Year	2	845.2	2.0948	0.1256
	Month	11	3001.9	7.4400	**<0.0001**
	Site*Year	6	1258.7	3.1197	**0.006**
	Site*Month	33	2185.4	5.4165	**<0.0001**
	Year*Month	19	1449.3	3.5920	**<0.0001**
	Site*Year*Month	56	1098.9	2.7235	**<0.0001**
	Error	207	403.5		
PO_4	PO_4				
	Site	3	26.0851	48.9747	**<0.0001**
	Year	2	9.4590	17.7592	**<0.0001**
	Month	11	12.2806	23.0569	**<0.0001**
	Site*Year	6	2.8725	5.3932	**<0.0001**
	Site*Month	33	6.7542	12.6809	**<0.0001**
	Year*Month	19	2.1501	4.0368	**<0.0001**
	Site*Year*Month	56	0.6903	1.2961	0.0993
	Error	207	0.5326		
TP	TP				
	Site	3	109.847	41.3489	**<0.0001**
	Year	2	43.156	16.2449	**<0.0001**
	Month	11	11.225	4.2253	**<0.0001**
	Site*Year	6	15.632	5.8842	**<0.0001**
	Site*Month	33	16.259	6.1203	**<0.0001**
	Year*Month	19	8.354	3.1448	**<0.0001**
	Site*Year*Month	56	6.347	2.3891	**<0.0001**
Error	Error	206	2.657		

df, degrees of freedom; MS, mean square; F, ratio of MS terms.
Significant effects denoted in bold.

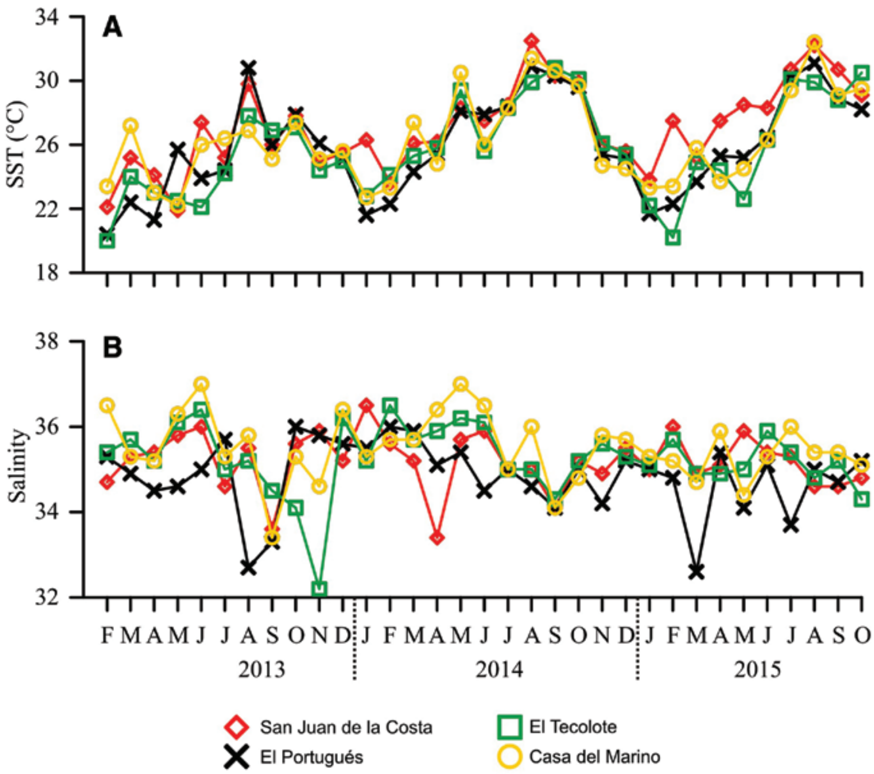

Figure 2: Hydrographic variables at four sites in the Gulf of California. (A) Surface seawater temperature (SST) and (B) salinity.

higher than those found during January and February 2014, January and March 2015 at Casa del Marino and in May to July 2014 at San Juan de la Costa and El Tecolote, and January and February 2015 at El Portugués ($p < 0.05$).

Succession of *Ulva* species

The macroalgal blooms in the four localities across Bahía de La Paz comprised eight species: *Ulva acanthophora (*Kützing) Hayden, Blomster, Maggs, P.C. Silva, Stanhope *et* J.R.Waaland, *Ulva clathratha* (Roth) C.Agardh, *Ulva flexuosa* Wulfen, *Ulva intestinalis* Linnaeus, *Ulva lactuca* Linnaeus, *Ulva lobata* (Kützing) Harvey, *Ulva nematoidea* Bory and *Ulva rigida* C. Agardh.

Ulva flexuosa was the only species found at El Portugués during the three sampling years and showed a seasonal pattern (Figure 4A). A succession of species was more evident at San Juan de La Costa and Casa del Marino. At the first of these sites, *U. rigida* was generally the only species observed in January; in February, *U. acanthophora* and *U. clathratha* appeared, and during March and April thalli of *U. lactuca* and *U. intestinalis* were also present. *Ulva nematoidea* and *U. lobata* were found only sporadically. The April–May bloom included all seven species. In June, *U. acanthophora, U. clathratha*, *U. intestinalis* and *U. lactuca* were no longer present, and the bloom was again dominated by *U. rigida*, which disappeared by the end of the year. A similar pattern was observed at Casa del Marino. At El Tecolote, the *Ulva* bloom was dominated by *U. rigida*, which appeared in December and persisted through the year. In March, *U. acanthophora*, *U. intestinalis, U. lactuca* and *U. lobata* were also found, but only sporadically until the end of the year.

Mean values of cover, recruitment and length of each of the eight species at the four localities during the 3 years of the study showed highly significant variation among locations, years and months, and these were mostly affected by the interactions between site and year, site and month, and year and month, as well as by the interaction among sites, years and months (Table 2), although there were more exceptions than with the physical and chemical variables.

Cover

The highest cover of *Ulva flexuosa* found at El Portugués during February and November 2013 was above 50%, and two times higher than in December 2013, January 2014 and February 2015 (Figure 4A). *Ulva rigida* had the highest cover

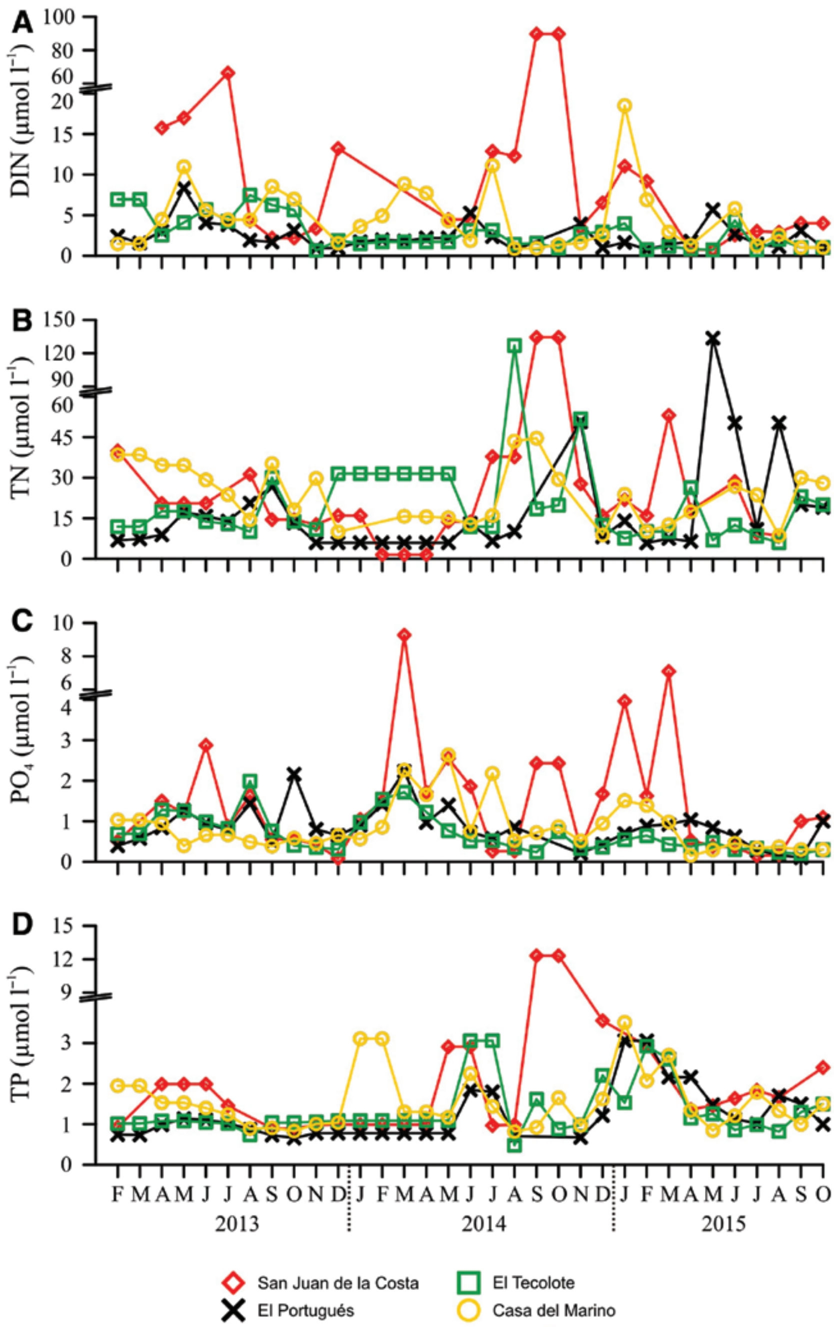

Figure 3: Nutrient concentration at four sites in the Gulf of California.
(A) Dissolved inorganic nitrogen (DIN), (B) total nitrogen (TN), (C) orthophosphate (PO_4) and (D) total phosphorus (TP).

at San Juan de la Costa during May 2013, March to May 2014 and April 2015 (Figure 4B). Total cover values at San Juan de la Costa and Casa del Marino during February and June 2013 and March to May 2014 were almost two times higher than the total cover found at these localities during the rest of the year (Figure 4B and C). At El Tecolote, cover values similar to those in the other localities were found only in February to April 2013 and, at all other times, the cover was below 20% (Figure 4D). *Ulva acanthophora* showed its highest values at Casa del Marino during January 2014 and 2015 ($p < 0.05$). The cover of the remaining species was variable and lower than 20% (Figure 4B–D).

Recruitment

The species with the highest recruitment biomass was *Ulva rigida*. The maximum value was found at Casa del

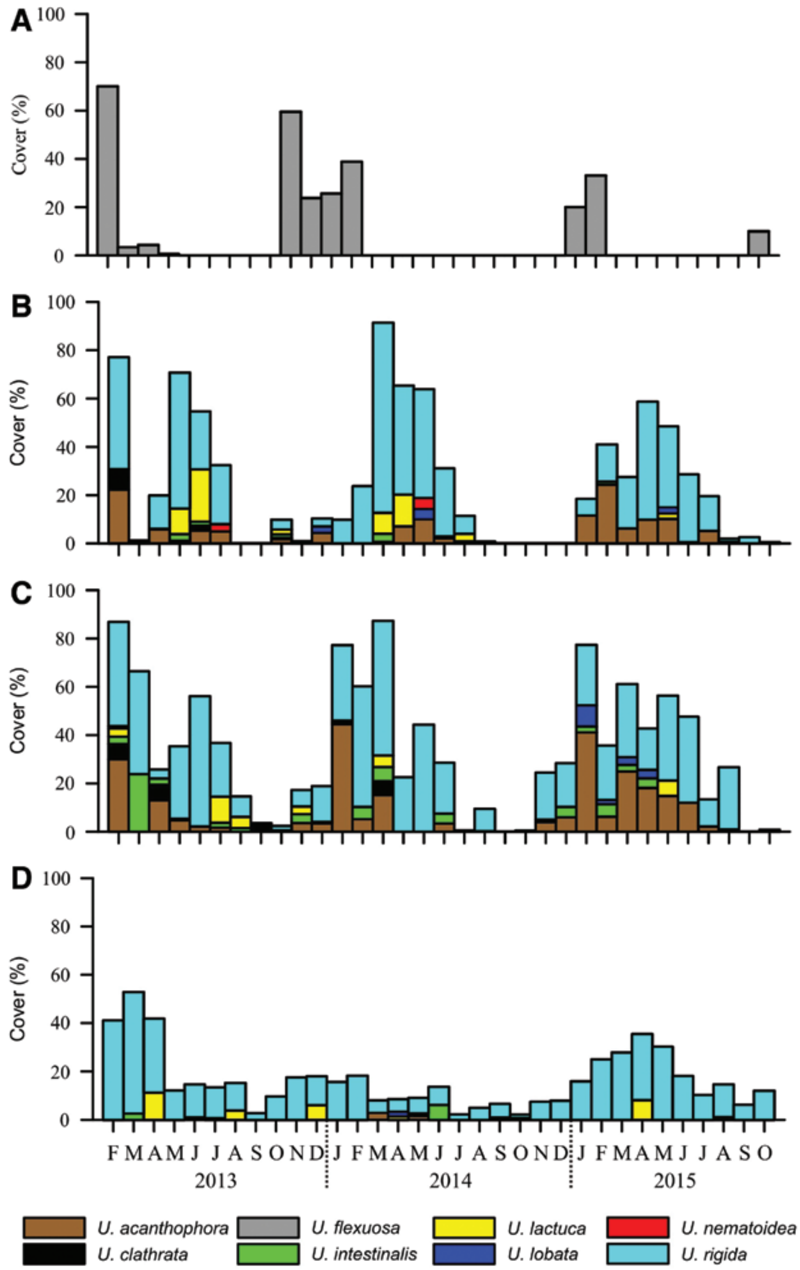

Figure 4: Presence and cover percentage of *Ulva* species at four sites in the Gulf of California. (A) El Portugués, (B) San Juan de La Costa, (C) Casa del Marino and (D) El Tecolote.

Marino in February 2013 and this was two times higher than the maximum values found during March 2013 and April 2014 at San Juan de la Costa and May 2014 at El Tecolote ($p < 0.05$). *Ulva acanthophora* also had high recruitment biomass at Casa del Marino during February 2013 and January and February 2014, and these values were two times higher than those found at San Juan de la Costa during February 2013 and 2014 ($p < 0.05$). The maximum recruitment biomass of *Ulva flexuosa* at El Portugués was found in February 2013 (Figure 5A–D).

Length

Ulva acanthophora was the longest *Ulva* species when present, particularly at San Juan de la Costa in March 2014 and at Casa del Marino from February to March 2015. The next longest species was *Ulva rigida*, which attained its greatest length at San Juan de la Costa during March, June and July 2013 and at Casa del Marino from February to May 2015. *Ulva flexuosa* was the shortest of the species when it was present ($p < 0.05$, Figure 6A–D).

Table 2: Results of MANOVA on *Ulva* species, among site, year, month and their interactions.

Interaction	df	*U. acanthophora*		*U. clathratha*		*U. flexuosa*		*U. intestinalis*		*U. lactuca*		*U. lobata*		*U. nematoidea*		*U. rigida*	
		F	p-Value	F	p-Value	F	p-Value	F	p-Value	F	p-Value	F	p-Value	F	p-Value	F	p-Value
Cover																	
Site	3	74.2	**<0.0001**	16.7	**<0.0001**	104.7	**<0.0001**	24.6	**<0.0001**	8.7	**<0.0001**	9.5	**<0.0001**	9.0	**<0.0001**	81.1	**<0.0001**
Year	2	13.1	**<0.0001**	24.1	**<0.0001**	12	**<0.0001**	3.7	**0.026**	10.4	**<0.0001**	7.1	0.001	4.9	**0.007**	1	0.355
Month	11	18.5	**<0.0001**	11.2	**<0.0001**	27.7	**<0.0001**	6.6	**<0.0001**	3.7	**<0.0001**	4.1	**<0.0001**	7.5	**<0.0001**	25.7	**<0.0001**
Site*Year	6	6.1	**<0.0001**	9	**<0.0001**	12.2	**<0.0001**	2.3	**0.032**	2.8	**0.012**	9.9	**<0.0001**	2.2	**0.039**	5.4	**<0.0001**
Site*Month	33	12.6	**<0.0001**	6.3	**<0.0001**	27.8	**<0.0001**	4.8	**<0.0001**	3.9	**<0.0001**	5.4	**<0.0001**	4.6	**<0.0001**	6.5	**<0.0001**
Year*Month	19	3.5	**<0.0001**	14.5	**<0.0001**	4.9	**<0.0001**	3.8	**<0.0001**	2.8	**<0.0001**	2.6	**<0.0001**	10.4	**<0.0001**	2.8	**<0.0001**
Site*Year*Month	57	2.7	**<0.0001**	7.8	**<0.0001**	4.9	**<0.0001**	2.9	**<0.0001**	4.4	**<0.0001**	2.6	**<0.0001**	6.1	**<0.0001**	3.1	**<0.0001**
Error	933																
Recruitment biomass																	
Site	3	32.9	**<0.0001**	5.9	**0.001**	17.0	**<0.0001**	10.4	**<0.0001**	32.0	**<0.0001**	7.2	**<0.0001**	11.0	**<0.0001**	42.7	**<0.0001**
Year	2	1.9	0.151	5.1	**0.006**	6	**0.003**	0.9	0.425	17.4	**<0.0001**	0.3	0.727	3.1	**0.047**	3.9	**0.022**
Month	11	11.5	**<0.0001**	6	**<0.0001**	4.9	**<0.0001**	1.7	0.080	11.3	**<0.0001**	1.9	**0.035**	5	**<0.0001**	14.1	**<0.0001**
Site*Year	6	2.5	**0.024**	4.6	**<0.0001**	6.1	**<0.0001**	1.1	0.362	15.5	**<0.0001**	0.6	0.720	3.1	**0.006**	1.4	0.221
Site*Month	33	7.8	**<0.0001**	4.5	**<0.0001**	4.9	**<0.0001**	1.6	**0.017**	11.5	**<0.0001**	1.9	**0.003**	5	**<0.0001**	8.8	**<0.0001**
Year*Month	19	1.5	0.092	7.8	**<0.0001**	3.5	**<0.0001**	1.7	**0.029**	14.8	**<0.0001**	1.5	0.071	6.4	**<0.0001**	2.2	**0.003**
Site*Year*Month	57	1.7	**0.001**	5.2	**<0.0001**	3.5	**<0.0001**	1.8	**0.001**	14.4	**<0.0001**	1.7	**0.002**	6.4	**<0.0001**	3.3	**<0.0001**
Error	395																
Length																	
Site	3	119.5	**<0.0001**	70.6	**<0.0001**	381.8	**<0.0001**	60.8	**<0.0001**	160.9	**<0.0001**	145.0	**<0.0001**	46.9	**<0.0001**	429.4	**<0.0001**
Year	2	10.3	**<0.0001**	56.9	**<0.0001**	40.6	**<0.0001**	9.1	**<0.0001**	45.4	**<0.0001**	7.5	**0.001**	10.4	**<0.0001**	43.9	**<0.0001**
Month	11	25.7	**<0.0001**	38.7	**<0.0001**	53.1	**<0.0001**	13.9	**<0.0001**	23.6	**<0.0001**	34.9	**<0.0001**	19.9	**<0.0001**	58.8	**<0.0001**
Site*Year	6	9.2	**<0.0001**	28.2	**<0.0001**	40	**<0.0001**	4.6	**<0.0001**	52.2	**<0.0001**	11.4	**<0.0001**	10.6	**<0.0001**	38.9	**<0.0001**
Site*Month	33	14.9	**<0.0001**	16.8	**<0.0001**	52.1	**<0.0001**	8.3	**<0.0001**	17.9	**<0.0001**	30.1	**<0.0001**	19.6	**<0.0001**	20.1	**<0.0001**
Year*Month	19	2.2	**0.002**	49.9	**<0.0001**	16	**<0.0001**	4.6	**<0.0001**	16.9	**<0.0001**	12.4	**<0.0001**	26	**<0.0001**	5.1	**<0.0001**
Site*Year*Month	57	3.4	**<0.0001**	21.7	**<0.0001**	15.9	**<0.0001**	5.7	**<0.0001**	13.8	**<0.0001**	17.2	**<0.0001**	25.6	**<0.0001**	5.1	**<0.0001**
Error	917																

df, degrees of freedom; MS, mean square; F, ratio of MS terms.
Significant effects denoted in bold.

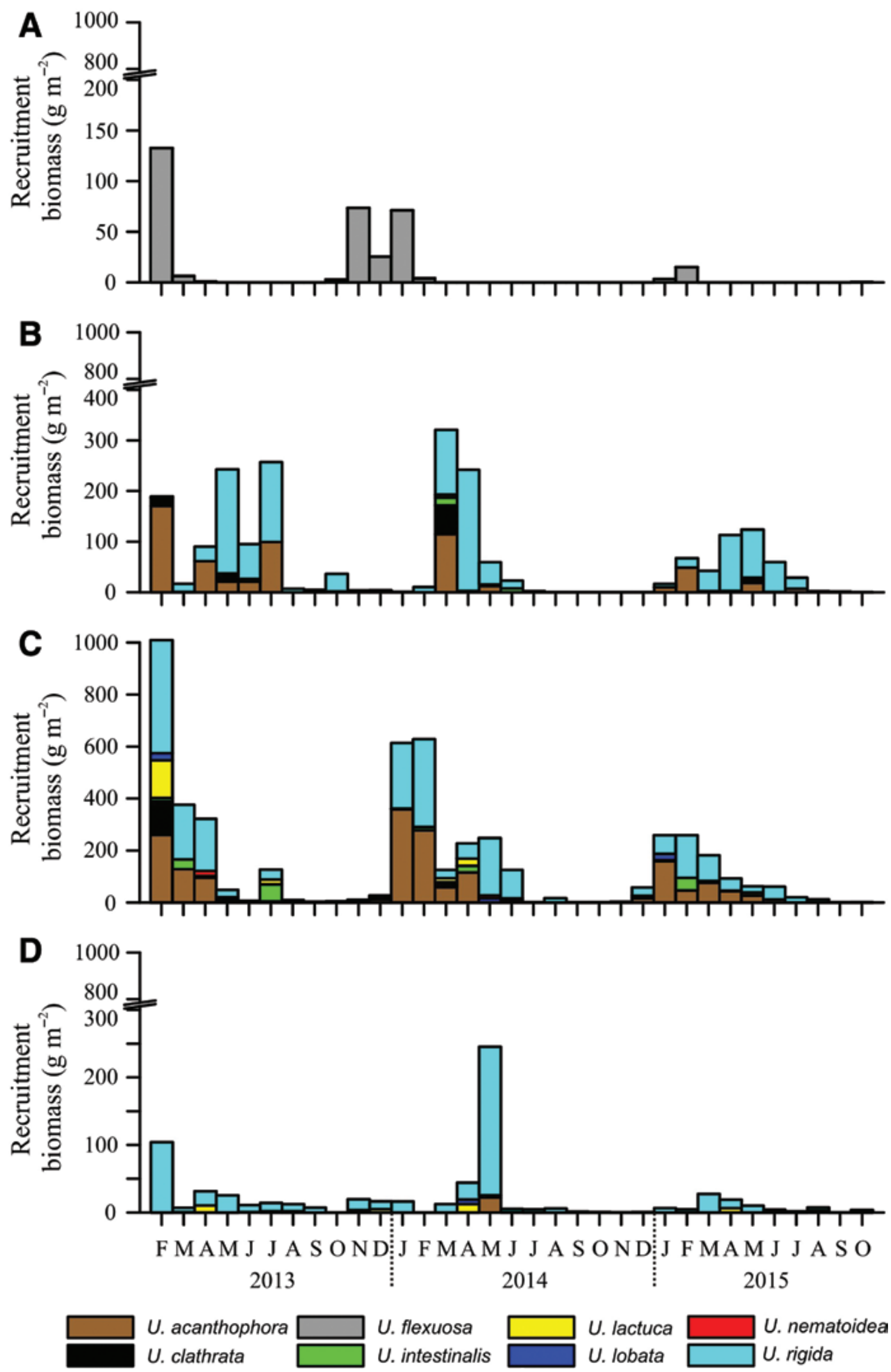

Figure 5: Recruitment biomass of eight species of *Ulva* at four sites in the Gulf of California. (A) El Portugués, (B) San Juan de La Costa, (C) Casa del Marino and (D) El Tecolote.

Biotic vs. environmental parameters

The graphical representation of the set of biological and environmental variables (PCA) showed that the first three factors accounted 65% of the cumulative variance (Figure 7). Factor 1 in the horizontal plane (32.7%) indicated that increases in DIN, TN and TP were associated with increases in recruitment and cover mainly of *Ulva acanthophora*. In contrast, increases in recruitment, length and cover of *Ulva flexuosa* were related to low concentrations of these nutrients. Factor 2 in the vertical plane (18.2%) suggested that increases in PO_4 were associated with increases in recruitment and length of *U. acanthophora*, as well as with increases in recruitment and cover of *Ulva rigida*, and

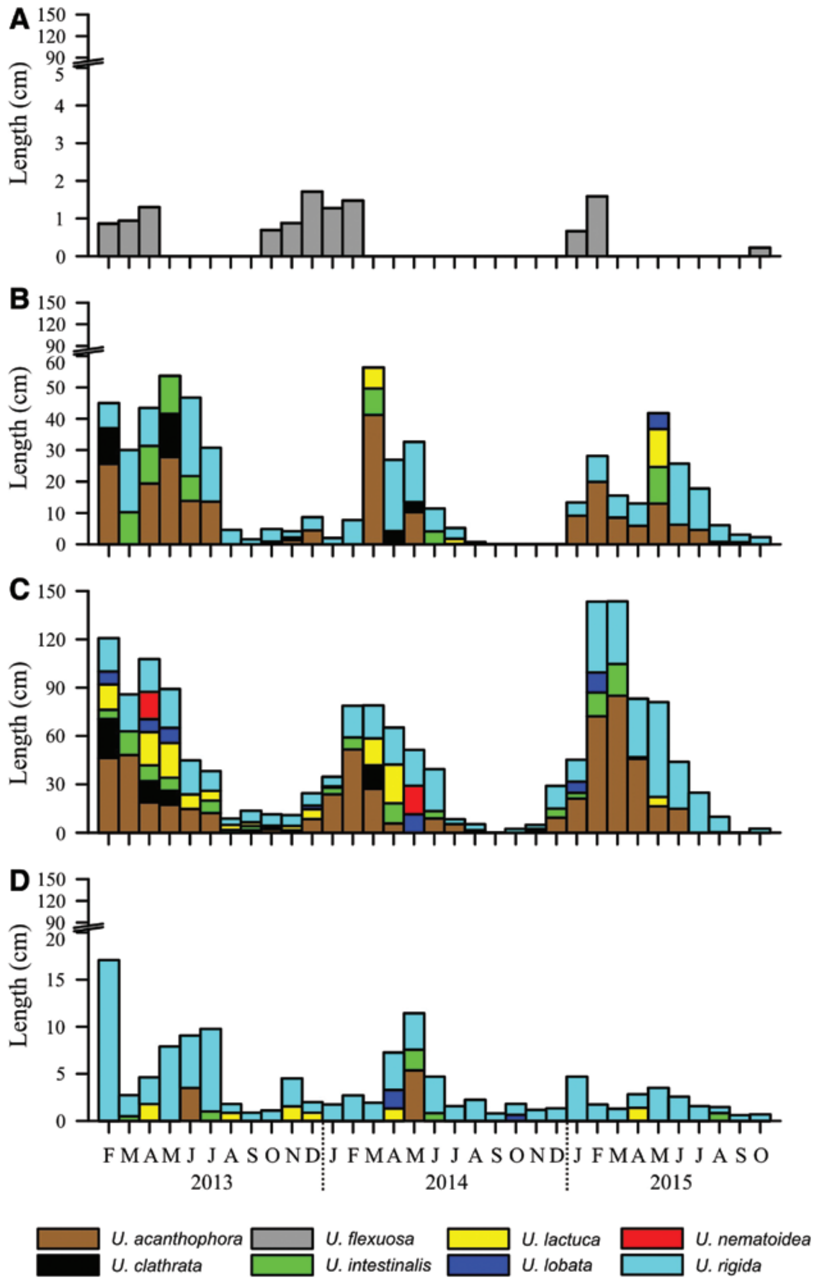

Figure 6: Length of *Ulva* species at four sites in the Gulf of California.
(A) El Portugués, (B) San Juan de La Costa, (C) Casa del Marino and (D) El Tecolote.

with the increase in length and cover of *U. flexuosa*. Factor 3 in the vertical plane (12.3%) showed that higher increases in temperature limited recruitment, cover and length of *U. acanthophora*, *U. flexuosa* and *U. rigida*.

Discussion

Species of the genus *Ulva* are common in Bahía de La Paz (Águila-Ramírez et al. 2005), an area characterised by a broad environmental variability, e.g. SST during summer season can reach 30°C while during winter it can descend to 20°C, as a consequence of its subtropical localisation (Cervantes-Duarte et al. 2001, Monreal-Gómez et al. 2001). This variability had been observed both within and between years. Consequently, some seasons have optimal environmental conditions for increasing the abundance of *Ulva* species, as previously reported by Águila-Ramírez et al. (2005). The localities of Casa del Marino and San Juan de La Costa with a high availability of a number of

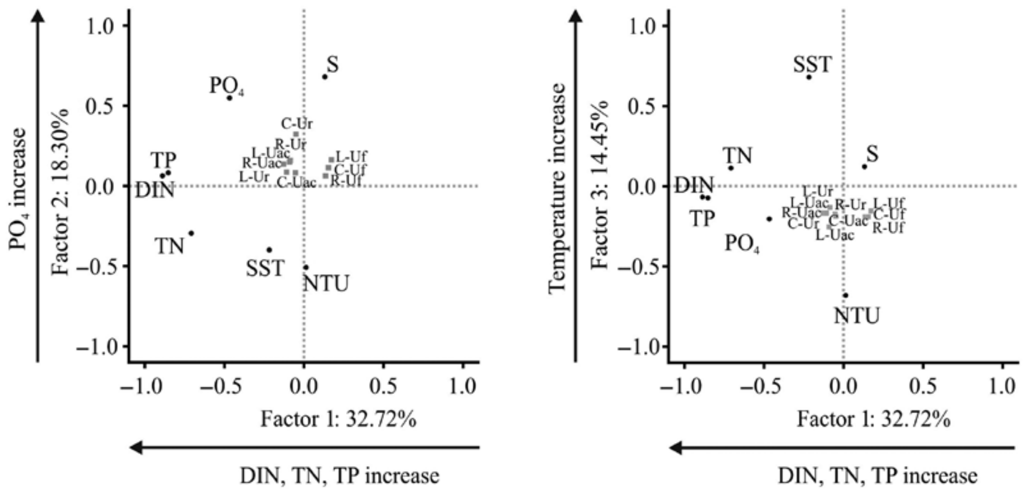

Figure 7: Principal component analysis (PCA).
(A) Factor 1 vs. Factor 2 and (B) Factor 1 vs. Factor 3. SST, Surface seawater temperature; S, salinity; NTU, turbidity; DIN, dissolved inorganic nitrogen; TN, total nitrogen; PO_4, orthophosphate; TP, total phosphorus; R-Uac, recruitment biomass of *Ulva acanthophora*; L-Uac, length of *U. acanthophora*; C-Uac, cover of *U. acanthophora*; R-Uf, recruitment biomass of *U. flexuosa*; L-Uf, length of *U. flexuosa*; C-Uf, cover of *U. flexuosa*; R-Ur, recruitment biomass of *U. rigida*; L-Ur, length of *U. rigida*; C-Ur, cover of *U. rigida*.

substrates (shells, coral fragments, boulders and residues of anthropogenic materials), shallow depth (<2 m) and small waves, allowed the largest number of *Ulva* species. This substrate type is suitable for the settlement of *Ulva* recruits, as observed in experimental assays where plastic, bamboo sticks, different types of ropes, mesh, rocks and sand served as substrate for the settlement of *Ulva prolifera* recruits in the Yellow Sea (Geng et al. 2015).

At El Portugués, the bloom included a single species, *Ulva flexuosa*. El Portugués is influenced to a greater extent by water currents and masses from the Gulf of California, a cyclonic gyre in deeper layers, which in turn causes an exchange of surface and subsurface water between the Gulf of California and Bahía de La Paz. This opening to the north also experiences waves of greater intensity than the localities in the interior portion of the bay (Obeso-Nieblas et al. 2008). *Ulva flexuosa* was found in the intertidal zone, an area with abundant rocky conglomerates and boulders where recruits attach, forming carpets up to 2 cm high in autumn and winter; the rugosity of these conglomerates and boulders likely facilitates the attachment of this small-thallus species, and it could be the reason why it is not found at the other localities studied.

Each species within the genus *Ulva* has particular substrate requirements for spore germination (Geng et al. 2015). In addition, coastal dynamics fluctuate throughout the year in this area. In winter (December to February) waves are intense; however, the morphology of this species (small tubular thalli) allows it to prosper on rocks where the waves break while the rest of the year (May to September) it is probably unfavourable because of the strong solar radiation typical of this time of the year. In addition, the winds from the south and southeast (Obeso-Nieblas et al. 2008) lead to the rocks being completely covered with sand and gravel, thus limiting the presence of *U. flexuosa* in these months.

Species succession is a common trait in any given environment. In the localities studied this succession was particularly evident at San Juan de La Costa and Casa del Marino where one of the two most abundant species (*Ulva acanthophora* and *Ulva rigida*) dominated over the other depending on the time of the year. The species *U. acanthophora* has been described as having temperate affinities (Casas-Valdez et al. 2000), a high presence and cover in late winter and spring, and decreasing progressively toward the summer when SST exceeded 25°C. *Ulva rigida* is considered to be a widely distributed species that shows a broad tolerance to solar radiation, temperature and salinity, which was evident as this species remained until the SST was above 30°C. Previous work in temperate regions has suggested that temperatures and irradiance in spring and summer foster spore germination and growth of *Ulva* (Lotze and Worm 2002, Sousa et al. 2007).

The least abundant species were *Ulva clathrata*, *Ulva intestinalis*, *Ulva lactuca*, *Ulva lobata* and *Ulva nematoidea* whose presence was sporadic with no obvious pattern, suggesting that these species were displaced by the abundance of the dominant species or because of some other environmental factors. Huo et al. (2015) reported that *U. prolifera*, *U. flexuosa* and *Ulva linza* were present in the winter season from December 2012 to April 2013. These authors contend that they probably did not observe a succession of these species as they expected because of the short period of time over which their observations were made, hence the importance of following-up blooms over long periods of time to observe the succession of species, as at San Juan de La Costa and Casa del Marino.

The high growth rate of *Ulva* and its high and diverse reproductive capacities explain why the species in this genus accumulates a large biomass (Liu et al. 2013, Huo et al. 2015). The biomass of *U. rigida* and *U. acanthophora* recruits fluctuated over the 3 years studied; however, it was always higher in winter and spring and decreased toward the autumn. Rosemary (2009) reported that the seasonal recruitment pulses and natural abundance of *Ulva* in a temperate locality were higher in late spring and summer, which was different from that observed in Bahía de La Paz, a subtropical environment. For the rest of the species in the bay, recruitment was considerably lower throughout the year and occurred at its greatest extent in spring.

Some studies mentioned that the temperature range of 10–25°C is suitable for the complete life cycle of *Ulva* species (Song et al. 2015). In San Juan de La Costa, Casa del Marino and El Tecolote, average temperature exceeded 20°C in all locations, which was favourable for the recruitment and blooming of Ulva, similar to findings reported by Liu et al. (2013) and Huo et al. (2015). Salinity is also an important factor in *Ulva* recruitment. Sousa et al. (2007) mentioned that germination and growth of the propagules already established was influenced positively by a salinity of 35, even under different nutrient and irradiance conditions. The highest recruitment biomass of *U. acanthophora* and *U. rigida* was found in a salinity range of 34.5–35.5 at the four localities of Bahía de La Paz.

Growth rates are regulated by solar radiation and temperature (Hurd et al. 2014), as well as by nutrient availability (Pedersen and Borum 1996). In the spring and early summer, temperature and salinity (25°C and 35°C) are optimal for growth within the bay, as suggested by Taylor et al. (2001) as temperatures from 25 to 30°C lead to rapid growth. Accordingly, *Ulva* blooms across the bay were obvious from late winter to early summer. In August and September, *Ulva* detached from the substrate, coinciding with a rise in SST >30°C and maximum solar radiation up to 1190.4 $\mu mol\ m^{-2}\ s^{-1}$, and entered a senescent stage, probably because these conditions were no longer optimal for growth.

Of all *Ulva* species, *U. acanthophora* exhibited the largest length. The maximum lengths were 300 and 81 cm at Casa del Marino and San Juan de La Costa, respectively, during winter. As previously discussed, this species is favoured by lower temperatures because of its temperate affinities. *Ulva rigida* attained its greatest length toward the spring and early summer in both localities (130 and 45 cm). At El Tecolote, *U. rigida* was smaller (<17 cm) than at San Juan de La Costa and Casa del Marino. This locality had a rocky platform that stretches over a greater shallow area, differing from the conditions in the two other localities. This substrate and the high desiccation observed might have been unfavourable for longer thalli although it allowed the species to be present. The high nutrient levels, probably originating from the Gulf of California upwelling waters in this pristine locality (Monreal-Gómez et al. 2001), were not limiting factors for the growth of *Ulva* thalli.

At San Juan de la Costa and Casa del Marino, the average concentration of nutrients (32.6 and 30.5 $\mu mol\ l^{-1}$ of TN and 2.8 and 1.5 $\mu mol\ l^{-1}$ of TP, respectively) were similar to or even higher than in coastal lagoons of the Gulf of California where macroalgal blooms have been observed (e.g. 14.2 and 1.1 $\mu mol\ l^{-1}$ TN and TP, respectively; Ochoa-Izaguirre et al. 2002).

The PCA showed that higher recruitment and cover of *U. acanthophora* were correlated with higher DIN, TN and TP concentrations, which has also been observed by Huo et al. (2015) who found a positive correlation between the abundance of a filamentous species of *Ulva* with certain concentrations of DIN (2.6–21.16 $\mu mol\ l^{-1}$), TN (17.2–32.6 $\mu mol\ l^{-1}$), PO_4 (0.7–1.8 $\mu mol\ l^{-1}$) and TP (1.1–2.9 $\mu mol\ l^{-1}$). These ranges are similar to those found in this study. High PO_4 concentrations (0.8, 2 and 6.4 $\mu mol\ l^{-1}$) were associated with an increase in recruitment (Sousa et al. 2007), which agrees with our observations at San Juan de La Costa where the highest phosphorus levels were found (2.8 $\mu mol\ l^{-1}$).

Ulva blooms in La Paz Bay were dominated by two of the eight species found. The dominant species (*U. rigida* and *U. acanthophora*) alternated through time, as the most suitable temperature conditions differ for each species. It was evident that succession, cover and recruitment of the different species of the *Ulva* blooms showed seasonal patterns related to temperature, and that cover and recruitment increase with nutrient concentrations.

These types of studies are relevant for coastal water management as overabundant nutrients under otherwise favourable environmental conditions can lead to nuisance macroalgal blooms, resulting in adverse effects. Given that nutrient concentrations are already high, nutrient sources should be monitored in order to control their levels and mitigate their effects on the environment.

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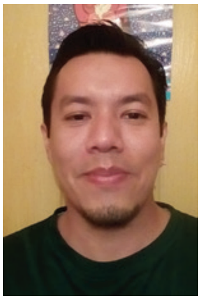
Bionotes



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