

# Seasonal phenology of *Sargassum liebmannii* J. Agardh (Fucales, Heterokontophyta) in an upwelling area of the Eastern Tropical Pacific



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## ABSTRACT

Seasonal changes in growth, biomass, abundance and reproduction of brown algae have been reported from subtropical and temperate regions, but there are very few reports from tropical regions, and none from the Eastern Tropical Pacific (ETP). *Sargassum liebmannii* is a common brown alga in the ETP at Bahía Salinas, a seasonal upwelling area in the northern Pacific coast of Costa Rica. We measured the length of ~50 individuals every two months from 2005 to 2007 and collected samples for reproductive analyses from 2008 to 2009. The growth rate of *S. liebmannii* peaked during the seasonal upwelling events (November to May), when minimum temperatures reached 15.5 °C and nutrient concentrations were high. During upwelling events, *S. liebmannii* grew from a few millimeters to over 1 m high, with a maximum mean growth rate of 0.68 cm d<sup>-1</sup> during the most intense upwelling period. Sexual reproduction occurred in the non-upwelling period. After attaining maximum size, *S. liebmannii* reproduces (June) and becomes detached from the substrate, floating in the bay and sometimes accumulating in nearby beaches. *Sargassum liebmannii* at this study site was absent in 2013 following a population outbreak of the black sea urchin, *Diadema mexicanum*.

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## 1. Introduction

Many species of macroalgae show marked variations in density, growth, and reproduction in seasonal upwelling regions (Diaz-Pulido and Garzón-Ferreira, 2002; Guimaraens et al., 2005) or highly seasonal areas (Ateweberhan et al., 2006). Only three studies on *Sargassum* seasonality in the tropics have been found, the Caribbean coast of Colombia (Camacho and Hernández-Carmona, 2012), Curaçao (Engelen et al., 2005a,b) and the Philippines (Ang, 1985). Many species of the brown macroalgae *Sargassum* (Order Fucales) show seasonal pattern related to temperature and nutrients in subtropical and temperate zones, e.g. in the Gulf of California, México (Espinoza and Rodríguez, 1987, 1989; Núñez-López and Casas-Valdéz, 1996, 1997; Rivera and Scrosati, 2006), Spain (Arenas and Fernández, 2000), Taiwan (Hwang et al., 2004), and France (Le Lann et al., 2012). At those sites most of the *Sargassum* species attain the highest growth rates during the warmer

months. Seasonal patterns of *Sargassum* phenology have yet to be reported from the Eastern Tropical Pacific.

*Sargassum* is an important primary producer in many shallow marine environments (Chung et al., 2010). This brown alga and organisms associated with it (mainly small crustaceans) serve as a food source for many vertebrates and invertebrates in the water as well as ashore (Viejo, 1999; Rooker et al., 2006). *Sargassum* species enhance habitat rugosity, provide surface for epibionts, and shelter for many organisms (Graham et al., 2009; Laffoley et al., 2011; Suárez-Castillo et al., 2013). Moreover, *Sargassum* can be harvested from their natural habitats or cultivated as human food and animal feed (Casas-Valdez et al., 2006; Graham et al., 2009; Marín et al., 2009), and as raw material for algininate production (Rodríguez-Montesinos et al., 2008).

The species in this study has been identified as *Sargassum liebmannii* (J. Agardh, 1847) and specimens at the Universidad de Costa Rica Herbarium (USJ) are recorded as *S. liebmannii*. However, recent work indicates that the species in question might in fact be *S. pacificum* (Cindy Fernández-García and Gabriela Andrade-Sorcía, personal communication). *S. liebmannii* is distributed from California to Colombia, including the Pacific coast of Central America (Setchell, 1937; Dawson, 1957, 1960, 1962; Fernández-García et al., 2011). This species is found along the Pacific coast of Costa

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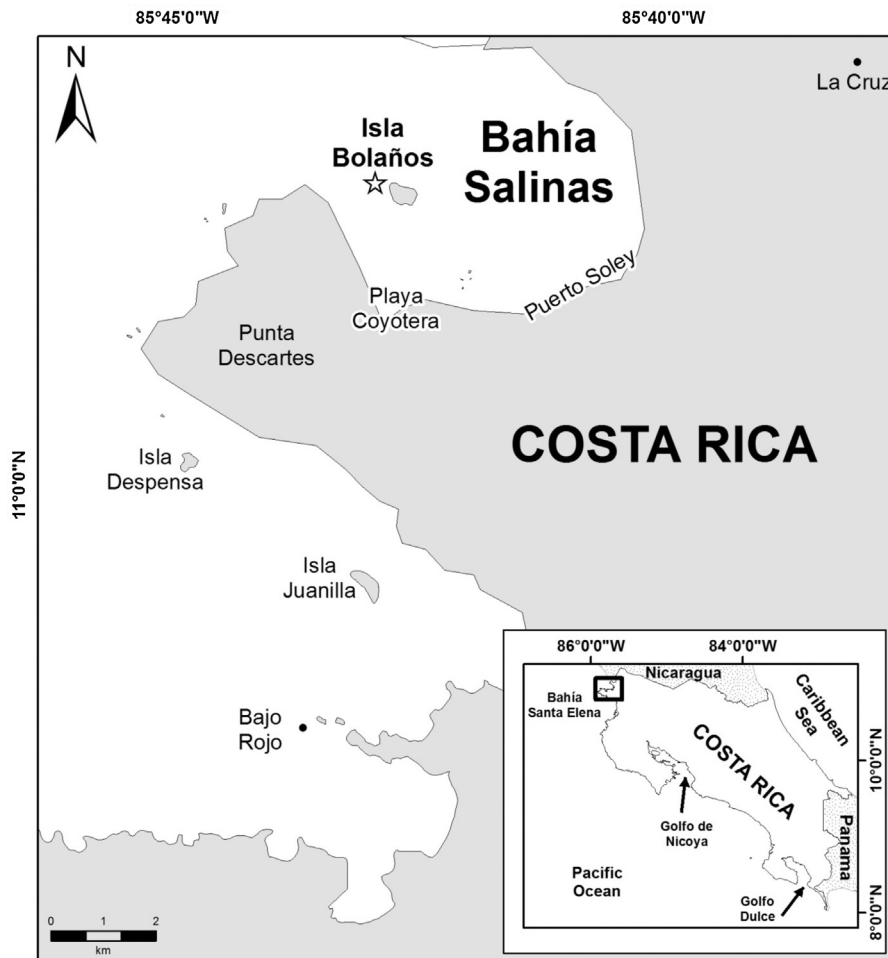


Fig. 1. Study site (star) at Bahía Salinas, Guanacaste, northern Pacific coast of Costa Rica.

Rica, from Bahía Santa Elena (Setchell, 1937), and Bahía Salinas (this study) in the north to Golfo Dulce (Taylor, 1945) in the south. It is most abundant on the northern section of the Pacific coast of Costa Rica, a seasonal upwelling region. There, we have observed that *S. liebmannii* grows to more than 1 m high, which is uncommon in the tropics. After attaining maximum growth the algae detach and drift on the ocean surface. *S. liebmannii* is important as flotsam, for several groups of associated animals, mainly small crustaceans, and as a food source for terrestrial shore animals, such as amphipods and insects (JC personal observation).

In this study we aimed to contribute to the knowledge of algal dynamics in the Eastern Tropical Pacific by determining the growth and reproduction patterns of the brown alga *S. liebmannii*. We studied this macroalgae over a 24-month period in a seasonal upwelling area of Costa Rica (Bahía Salinas) and related its phenology to temperature variations linked to upwelling events.

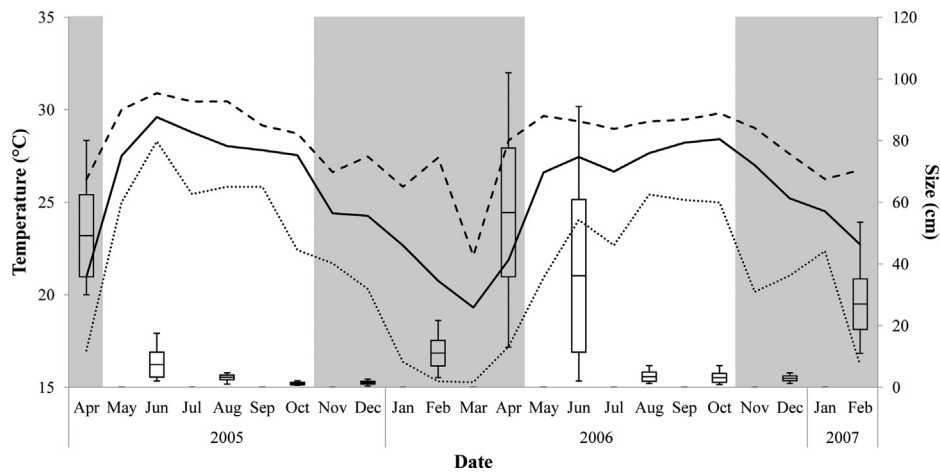
## 2. Materials and methods

The study was carried out near the Refugio Nacional de Vida Silvestre Isla Bolaños (National Wildlife Refuge), Bahía Salinas, on the northern Pacific coast of Costa Rica, 11°03'06.6" N 85°42'53.6" W (Fig. 1). Depth at this site is approximately 5 m at high tide (3 m tidal range). Water temperature, as a proxy for upwelling events, was recorded at the study site every 30 min with Hobo® Temp sensors, from April 2005 to February 2007.

Every two months from April 2005 to February 2007, algal thallus length was measured (defined as the length between the base

of the stipe and the tip of the longest primary branch) of around fifty randomly selected thalli of *S. liebmannii* in a 1.5 m<sup>2</sup> area. Average daily growth rate was determined by dividing the change in length by the number of days elapsed between measurements. The reproductive cycle of *S. liebmannii* was analyzed by haphazardly collecting a representative amount of thalli (from the holdfast) in the field every two months from February 2008 to August 2009. Samples were transferred to the laboratory where they were kept frozen until processing. Frequency of collected thalli that were reproductive and those with globose air bladders (vesicles) which are necessary for flotation was calculated. Abundance of reproductive receptacles and vesicles, was also determined for each thallus collected, as the percentage area of the thallus that was covered by either receptacles or vesicles in reference to the total area of each thallus. Subsequently, five thalli were randomly selected and mean length and number of stipes per thallus were determined. Furthermore, length and width of three blades from the middle section of each branch of these five thalli were measured (blade area = length × width). When fertile branches were found in these five individuals the length of ten random receptacles was measured.

Correlations were carried out in R (R Development Core Team, <http://www.R-project.org>) to analyze the relationship between length and multiple variables (temperature, receptacle and vesicle abundance, and number of stipes per thallus). Non-parametric Kruskal–Wallis tests were carried out to analyze variability of length, reproductive and vesicle abundance, and number of stipes per thallus among different measurement dates from *in situ* and



**Fig. 2.** Mean (solid line), minimum (dotted line), and maximum (dashed line) monthly *in situ* water temperature, and average (mid line in box), standard deviation (box) and minimum–maximum (lines) length of *Sargassum liebmannii* at Bahía Salinas, Guanacaste, northern Pacific coast of Costa Rica.

collected samples (as data were not normal, despite Box Cox and other transformations carried out).

**3. Results**

**3.1. Vegetative growth**

A total of 567 individuals of *S. liebmannii* were measured *in situ*, with an overall mean length of  $16.5 \pm 21.8$  cm (SD). Minimum length was 0.4 cm (December 2005), and maximum length was 102.0 cm (April 2006). Mean length varied seasonally ( $H=486.3$ ;  $df=11$ ;  $p<0.05$ ), with maximum lengths found during April (2005 and 2006) and shortest thalli observed in August, October, and December (Fig. 2). In general, longer thalli occurred at lower temperatures and shorter thalli at higher temperatures ( $r=-0.45$ ;  $p<0.05$ ). Overall, thalli were longer in 2006 than 2005 ( $H=56.2$ ;  $df=1$ ;  $p<0.05$ ). The highest growth rate was found between February and April 2006 ( $0.68 \text{ cm d}^{-1}$ ), a two to four fold increase from the growth rate between December and February (December 05–February 06 =  $0.17 \text{ cm d}^{-1}$  and December 06–February 07 =  $0.32 \text{ cm d}^{-1}$ ).

Mean number of stipes per thallus (2008–2009 sampling) was  $4 \pm 2$  (SD) (Min = 1; Max = 9;  $N=43$ ). Number of stipes varied according to sampling date ( $F=9.5$ ;  $df=8$ ;  $p<0.05$ ), with more stipes occurring between February and June (Table 1), and longer thalli tending to have more stipes ( $r=0.39$ ;  $p<0.05$ ). No variation was found between sampling years ( $H=2.6$ ;  $df=1$ ;  $p>0.05$ ). Mean blade length ( $\pm$ SD) was  $3.0 \pm 1.5$  cm ( $n=401$ ), width  $0.8 \pm 0.4$  cm, and estimated blade area  $2.6 \pm 1.9 \text{ cm}^2$ . Blades showed variation in length, width, and area among sampling dates, with longer blades present in February and April ( $H=61.1$ ;  $df=8$ ;  $p<0.05$ ), wider

blades in February ( $H=101.3$ ;  $df=8$ ;  $p<0.05$ ), and larger blades also found in February ( $H=78.4$ ;  $df=8$ ;  $p<0.05$ ) (Table 1).

**3.2. Reproduction**

Receptacle abundance varied among sampling dates ( $H=97.0$ ;  $df=8$ ;  $p<0.05$ ) ( $n=106$ ), with marked reproductive peaks evident in June of both 2008 and 2009 (Fig. 3a). Frequency of reproductive thalli was also highest during June of both years (Fig. 3b). Longer thalli tended to have more receptacles ( $r=0.74$ ;  $p<0.05$ ). Receptacle length varied among sampling dates ( $H=9.5$ ;  $df=3$ ;  $p=0.02$ ), yet no clear trend was discernable and mean lengths were similar (Table 1). Air vesicle abundance also varied among sampling dates (February 2008–August 2008) ( $H=42.3$ ;  $df=3$ ;  $p<0.05$ ), peaking prior to reproduction when thallus length was highest, and declining during the reproductive period (Fig. 3c). Frequency of thalli with vesicles followed the same pattern (Fig. 3d). No significant correlation was found between receptacle and vesicle abundance ( $r=0.22$ ;  $p=0.053$ ).

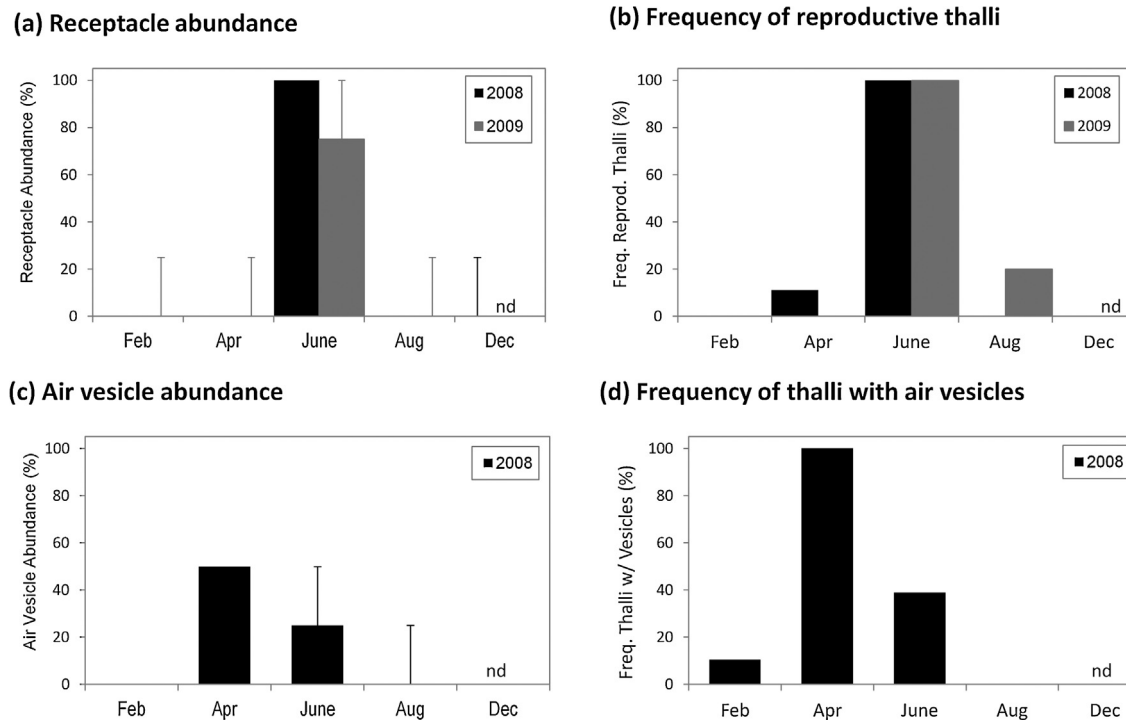
**4. Discussion**

*Sargassum liebmannii* displayed seasonal growth and reproduction patterns at Bahía Salinas, which correlated with seasonal upwelling on the northern Pacific coast of Costa Rica. This study is the fourth report of marked seasonality for *Sargassum* in a tropical region (Ang, 1985 in the Philippines, Engelen et al., 2005a,b in Curaçao, and Camacho and Hernández-Carmona, 2012 in Colombia), and the first for the Eastern Tropical Pacific. Thalli length was related to water temperature, with minimum lengths occurring during warmer months at the end of the year before the

**Table 1**  
Mean  $\pm$  SD (N) blade length and width, stipes per thallus, and receptacle length of *Sargassum liebmannii* at Bahía Salinas, North Pacific coast of Costa Rica.

Date	Blade length (cm)	Blade width (cm)	Stipes per thallus	Receptacle length (cm)
February 08	$3.7 \pm 1.8$ (60)	$0.9 \pm 0.2$ (60)	$4 \pm 1$ (5)	np
April 08	$3.0 \pm 1.2$ (62)	$0.7 \pm 0.2$ (62)	$4 \pm 2$ (5)	np
June 08	$2.2 \pm 0.9$ (62)	$0.7 \pm 0.3$ (62)	$4 \pm 1$ (5)	$0.5 \pm 0.1$ (10)
August 08	$2.3 \pm 1.0$ (15)	$0.6 \pm 0.1$ (15)	$1 \pm 0$ (5)	$0.6 \pm 0.1$ (50)
December 08	$2.7 \pm 1.0$ (14)	$0.5 \pm 0.2$ (14)	$2 \pm 1$ (5)	np
February 09	$3.7 \pm 1.8$ (68)	$1.0 \pm 0.6$ (68)	$5 \pm 1$ (5)	np
April 09	$3.4 \pm 1.6$ (39)	$0.7 \pm 0.4$ (39)	$6 \pm 2$ (5)	np
June 09	$2.3 \pm 0.8$ (51)	$0.6 \pm 0.2$ (51)	$3 \pm 1$ (5)	$0.5 \pm 0.1$ (27)
August 09	$2.5 \pm 1.3$ (29)	$0.8 \pm 0.3$ (29)	$3 \pm 0$ (5)	$0.5 \pm 0.2$ (3)

np, none present; na, not applicable.



**Fig. 3.** Mean ( $\pm$ SD) abundance of (a) receptacles and (b) frequency of reproductive *Sargassum liebmannii* thalli collected from February 2008 to August 2009, and abundance of (c) air vesicles and (d) frequency of thalli with vesicles from February to August 2008 at Bahía Salinas, northern Pacific coast of Costa Rica. n.d. = none detected.

start of the upwelling, and maximum lengths in April at the end of the upwelling (following decreased temperatures). Increases and decreases in thallus length, blade length and area were abrupt. Seasonal growth of *Sargassum* species has also been found previously in temperate regions (Arenas and Fernández, 2000; Wernberg et al., 2000; Yoshida et al., 2004), and from areas with extreme seasonal changes (Ateweberhan et al., 2006). The growth rate of *S. liebmannii* accelerated and peaked during the coldest months at Bahía Salinas. Even though the growth rates during the upwelling season at Bahía Salinas were very high, they were an underestimation of growth potential of *S. liebmannii* in the study area, since the bimonthly measurements carried out do not account for any loss of algal material due to herbivory or cellular death. Similar growth patterns of two other species of *Sargassum* have also been observed in seasonal upwelling regions of the tropical Caribbean of Colombia (Camacho and Hernández-Carmona, 2012). The growth rate of *Sargassum* spp. was also found to be highest during the coldest months at sites in the Red Sea with extreme weather conditions (Ateweberhan et al., 2006), the subtropical site of Bahía Concepción (Núñez-López and Casas-Valdéz, 1996), and La Paz, Gulf of California (Muñetón-Gómez and Hernández-Carmona, 1993; Rivera & Scrosati, 2006; Rodríguez-Montesinos et al., 2008). At higher latitudes the pattern appears to switch to highest *Sargassum* growth during the warmest months, as in Spain (Arenas and Fernández, 2000), Denmark (Wernberg et al., 2000), Japan (Yoshida et al., 2004), and France (Le Lann et al., 2012). In Taiwan, one of the four *Sargassum* species studied had highest biomass accumulation in winter, while the other species peaked in the warmest months (Hwang et al., 2004). Ang (1985), working in a tropical environment, found seasonal cycles for two species of *Sargassum* in the Philippines, as opposed to the other tropical studies. Phenology was related to annual nutrient cycles, with fastest growth during the warmest month when nutrient levels were highest.

At Bahía Salinas, *S. liebmannii* reproduced shortly after attaining maximum thallus length in June, when water temperature was

warmest, and air vesicle abundance diminished. Consistently, Wernberg et al. (2000) found almost no air vesicles on reproductive branches of *Sargassum muticum*. After attaining maximum length and reproduction, the thalli stopped growing, and eventually became detached from the substrate. Núñez-López and Casas-Valdéz (1996) found that the *Sargassum* species they studied also deteriorated after attaining maximum growth and reproduction. During the non-upwelling season at Bahía Salinas thalli size was minimum, mainly in August and October. It is still unclear if the individuals found represent a new cohort from sexual reproduction or if, in fact, there was an annual and perennial part of the thallus as found for *S. muticum* in Denmark (Wernberg et al., 2000). Camacho and Hernández-Carmona (2012) indicated that *Sargassum* species begin to grow from new recruits and from the remains of holdfasts in Colombia. Engelen et al. (2005a,b) found that in shallow populations sexual recruitment is important as well as holdfast re-growth after storms in Curaçao. Kendrick and Walker (1995) reported that *Sargassum* propagules disperse very short distances (most <1 m) and survival of recruits was exceedingly low. As *S. liebmannii* had a short reproductive period, and low reproductive output, it is likely that the abundance of short thalli observed at Bahía Salinas relatively soon after reproduction represented a perennial part of the thalli and not sexual recruits. Analysis of herbarium material of *S. liebmannii* from the Universidad de Costa Rica Herbarium (USJ) provided a basis for comparing the results from this study with other locations within Bahía Salinas. There was a lack of reproduction found in herbarium samples from Isla Despensa (Herbarium sample USJ-73641, 11°00'09" N 85°44'55" W) and Isote (USJ-73593, 11°02'55" N 85°44'33" W) collected in October 2004, which is congruent with results found in this study. Abundance of vesicles and lack of receptacles in April 2005 at Isla Bolaños (study site, USJ-73574, 11°03'02" N 85°42'43" W) and Bajo Rojo (USJ-73577, 10°56'57" N, 85°44'16" W) were also in accordance with the results of this study. However, the lack of vesicles and abundance of receptacles on the same date at Isla Juanilla (USJ-73661, 10°58'49" N,

85°43'02" W) may indicate that reproduction there was earlier than at the other two sites. Isla Juanilla samples were from 3 to 4 m depth while Bajo Rojo samples were from a 12 m depth, and Isla Bolaños samples were from a 6 to 7 m depth. This may indicate that at shallower sites reproduction might occur earlier than at deeper sites, where temperature was lower. Also, reproduction peaks may vary among sites due to the different intensity of the upwelling at each site. Isla Juanilla, a more protected site from upwelling may get warmer before the other sites. Further studies, including more sites and long term monitoring, are needed to determine the reproductive patterns of *S. liebmanni* within a broader environmental and geographical range.

At the end of the upwelling season, the algae detached from the substrate and floated in drifting mats throughout Bahía Salinas. A series of organisms, mainly small crustaceans, had been observed associated with the drifting *Sargassum*. Part of the material left the bay while the rest accumulated on nearby beaches. The accumulated algae on the beach were colonized by terrestrial and beach invertebrates, such as amphipods and insects (JC, personal observation).

During 2011–2012 there was an outbreak of the black sea urchin, *Diadema mexicanum*, at the study site (and other sites in Bahía Salinas). This was an extreme event that had not been observed in the previous 10 years that the area has been visited regularly. Densities of 6 ind m<sup>-2</sup> were observed (A.N. Suárez-Castillo, personal communication), higher than what has been previously recorded in the northern Pacific region of Costa Rica (0.20–2.19 ind m<sup>-2</sup>; Alvarado et al., 2012) and nearby southern Pacific coast of Nicaragua (0.04–1.10 ind m<sup>-2</sup>; Alvarado et al., 2011). The unprecedented increase of this herbivorous invertebrate resulted in an intense grazing pressure on *S. liebmanni*, and a shift from algal dominated substrate to bare substrate with practically no type of algae. This might represent a phase shift from an algae-dominated to a sea urchin dominated system. The disappearance of ecosystem engineers (specifically algae) by urchin herbivory has been reported for *Sargassum* forests in the Gulf of California, México (Aburto-Oropeza et al., 2008; A.N. Suárez-Castillo, Personal communication) and Japan (Haraguchi and Sekida, 2008). The losses of these seaweed forests may have implications in the decline of marine biodiversity and fisheries resources associated with them.

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