Effect of salinity on growth of the green alga *Caulerpa sertularioides* (Bryopsidales, Chlorophyta) under laboratory conditions

Efecto de la salinidad sobre el crecimiento del alga verde *Caulerpa sertularioides* (Bryopsidales, Chlorophyta) en condiciones de laboratorio

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ABSTRACT

Background. Salinity, temperature, nutrients, and light are considered essential parameters to explain growth and distribution of macroalgal assemblages in coastal zones. **Goals**. In order to evaluate the effect of salinity on the growth properties of *Caulerpa sertularioides*, we conducted this study under laboratory conditions to find out how salinity affects the distribution of this species in coastal tropical environments. **Methods**. Five ranges of salinity were used for the experiments (15, 20, 25, 30, and 35 ppt), simulating *in situ* salinity conditions on the south Pacific Coast of Colombia. The culture was grown in an environmental chamber with controlled temperature and illumination, and a 12:12 photoperiod. The following growth variables were measured weekly: wet biomass, stolon length (cm), number of new fronds and rhizomes. In the experimental cultures, growth (increase in wet biomass and stolon length) was calculated as the relative growth rate (RGR), expressed as a percentage of daily growth. **Results**. Significant differences ($p < 0.001$) were found between 15 ppt and the remaining treatments (20, 25, 30, and 35 ppt). The highest growth rates were recorded at 25 ppt (4.82 % d^{-1}), while at 15 ppt, whitening and progressive deterioration of *C. sertularioides* fragments were observed. These results are consistent with the natural habitat of *C. sertularioides* in Tumaco Bay (Nariño, Colombia), where it is found in areas with average salinities of 24 ppt during its annual cycle. **Conclusions**. The physiological responses obtained in this study will be valuable in exploring possible effects of environmental conditions on the growth and distribution of *Caulerpa* in tropical estuaries.

Key words: Algal growth, *Caulerpa sertularioides*, distribution, indoor culture, salinity.

RESUMEN

Antecedentes. Salinidad, temperatura, nutrientes y luz se consideran parámetros esenciales para explicar el crecimiento y la distribución de las comunidades de macroalgas en la zona costera. **Objetivos**. El objetivo de este estudio fue evaluar el efecto de la salinidad sobre las propiedades de crecimiento de *Caulerpa sertularioides*. **Métodos**. Cinco rangos de salinidad fueron utilizados para los experimentos (15, 20, 25, 30 y 35 ppt), simulando las condiciones de salinidad encontradas en la costa del Pacífico sur de Colombia. El cultivo se realizó en una cámara ambiental con temperatura e iluminación controladas, manteniendo un fotoperiodo 12:12. Se midieron semanalmente variables tales como, biomasa húmeda, longitud estolón (cm), número de hojas nuevas y rizomas. En el laboratorio, el crecimiento se calculó como la tasa de crecimiento relativo (RGR), expresada como porcentaje de crecimiento diario. **Resultados**. Se encontraron diferencias significativas ($p < 0.001$) entre el tratamiento de 15 ppt y los restantes (20, 25, 30 y 35 ppt). Las tasas de crecimiento más altas se registraron a 25 ppt (4.82% d-1), mientras que a 15 ppt se observó blanqueamiento y el deterioro progresivo de los fragmentos de *C. sertularioides*. Estos resultados son consistentes con el hábitat natural de *C. sertularioides* en la Bahía de Tumaco (Nariño, Colombia), donde la especie se encuentra en áreas con salinidades promedio de 24 ppt en su ciclo anual. **Conclusiones**. Las respuestas fisiológicas obtenidas en este estudio son valiosas para explorar posibles efectos de las condiciones ambientales sobre el crecimiento y la distribución de *Caulerpa* en estuarios tropicales.

Palabras clave: *Caulerpa sertularioides*, crecimiento de algas, cultivos in vitro, distribución, salinidad.

INTRODUCTION

Macroalgae of the *Caulerpa* genus (Chlorophyta: Bryopsidales) are of interest in the marine environment for several reasons. The high growth rates that some species exhibit, and their ability to propagate from asexual fragments have generated serious negative impacts on natural communities (Biber & Irlandi, 2006; Glardon *et al*., 2008; Pérez-Ruzafa *et al*., 2012). Three species, *C. taxifolia* (M. Vahl) C. Agardh, *C. brachypus* Harvey and *C. racemosa* (Forsskål) J. Agardh, originally found in warm tropical waters grow rapidly and are therefore classified as invasive plants (Klüser *et al*., 2004; Lapointe & Bedford, 2010). The factors that determine growth have been evaluated for several *Caulerpa* species (Khou *et al*., 2007; Theil *et al*., 2007; Burfeind & Udy, 2009; Guo *et al*., 2015). Salinity and temperature, together with nutrients and light, are considered essential parameters for the further cultivation of seaweed on a large scale (Scrosati, 2001; Lapointe & Bedford, 2010). Furthermore, physiological responses of *Caulerpa* to those abiotic parameters are used to discuss the implications for the management of this green alga for possible invasions (West & West, 2007; Lirman *et al*., 2014). Little is known, however, about the impact of salinity on the growth of C. *sertularioides* in tropical environments, such as the Colombian Pacific, where oceanographical conditions are constantly changing due to extensive river discharges and high precipitation patterns along the coast (Tejada *et al*., 2003). Particularly, on the Pacific coast of Colombia, *C. sertularioides* inhabits intertidal and shallow subtidal areas (Peña, 1998; 2008). No seasonality of natural populations was registered; however, great biomass was observed during low rainfall season within creeks along the Bay of Tumaco (Marin & Peña, 2014). Unlike other species within this genus, such as *C. taxifolia* and *C. racemosa*, there are several studies that address their tolerance to different environmental conditions and their conditions as invasive plants (Piazzi *et al*., 2001; Lirman *et al*., 2014). Osmotic acclimatization in response to changes in salinity is a fundamental tolerance mechanism that conserves the stability of the intracellular medium and is therefore essential to maintain an efficient functional state in the cells (Kirst, 1990; Peña *et al*., 1999; Ospina *et al*., 2006). It has been suggested that algae can regulate their cell volume by modifying the internal water potential in response to changes in salinity (Goulard *et al*., 2001; Eggert *et al*., 2007). Although most marine algae can tolerate fluctuations in salinity over the short term, large variations of this parameter can significantly affect some biochemical processes involved in photosynthesis and growth, altering the biomass, distribution, and productivity of a great number of species (Sousa *et al*., 2007; Choi *et al*., 2006; Theil *et al*., 2007). Those results demonstrated the plasticity and adaptation of *Caulerpa* species to different salinity gradients compared to other siphonous algae and, therefore, their capacity to spread out in shallow coastal environments.

The aim of this study is to evaluate growth conditions under different salinity conditions of the green alga *C. sertularioides* and its effect on the distribution and colonization of the species in the estuary.

MATERIALS AND METHODS

Culture conditions and experimental design. Fragments of *C. sertularioides* were brought from Tumaco Bay, Pacific coast of Colombia (1° 45' - 2° 00' N; 78° 30' - 78° 45' W). The bay comprises a 350 km^2 area with depths varying between 0 and 50 m (Tejada, 2002). Algal fragments were collected from the intertidal zone**,** during low tide and stored in paper towels moistened with seawater, packed in polyethylene bags and stored in a polystyrene icebox until transportation to the laboratory**,** according to West and Calumpong (1988). Fragments were cleaned of other benthic materials (sand, shell fragments, etc.) and kept in an environmental chamber with average temperatures of 27 ± 0.37 °C and controlled illumination (40-50 µmol photons m^{-2} s^{-1}). A 12:12 cycle of light/darkness was maintained during two (2) weeks for their acclimation. Material for subsequent experiments was then selected from these fragments. Fragments of *C. sertularioides* consisted of a basal portion (stolon), rhizome and 3-4 erect axes (fronds); fresh weight was between 0.2 and 2.0 g and was calculated at the beginning of the experiments (West & West, 2007). Five ranges of salinity were used for the experiments (15, 20, 25, 30, and 35 ppt). These salinities were chosen after examination of historical data of salinity recorded for Tumaco Bay by the oceanographical and Hydrological Research Center of the Colombian Army at the Pacific coast, located in the Port of Tumaco (Tejada *et al*., 2003). Six replicates of each salinity range were set up and the experiment was repeated twice, with a culture period of 4 (four) weeks each time, and measurements taken every 8 days. Mini-aquaria of 0.5 L capacity were filled with artificially filtered seawater enriched with Provasoli, stirred with aerators (modified by West & McBride, 1999) (10 ml L^{-1}), and changed weekly.

A one-way ANOVA (factor = salinity) was done to test for significant differences (5%) in total new growth. Data were tested for homogeneity of variances using Cochran's test. Where significant differences were found, Tukey's HSD test was used for means comparison. The R statistical package version 2.12.0 and SPSS 17.0 were used for the analyses.

Analysis of algal growth. The following growth variables were measured weekly: wet biomass, stolon length (cm), and number of new fronds and rhizomes. In the experimental cultures, growth (increase in wet biomass and stolon length) was calculated as the relative growth rate (RGR), expressed as percent daily growth, applying the following equation used by different authors (Areces, 1995; Anderson *et al*., 1997; Marinho-Soriano *et al*., 2002): RGR = $[(W_f/W_i)^{1/t} - 1] \times 100$, where RGR = relative growth rate, W_f = final wet weight, final length, W_i = initial wet weight, initial length; t = time interval elapsed between the two observations.

RESULTS

Salinity had a significant effect on the growth of *C. sertularioides* (p <0,001; Table 1; Figs 1a- b) during the culture period. The highest growth rates in terms of wet biomass during the culture period occurred for salinities of 25 and 30 ppt, with mean values of 2.262 ± 0.242 % d^{-1} and 1.408 ± 0.215 % d^{-1}, respectively (mean ± SD, n = 18), that remained constant during the experiment. The lowest growth rates were recorded for salinities of 15 and 35 ppt, which had growth rates of around 1% d^{-1} and lower. At a salinity of 15 ppt, growth rates were negative as a result of the progressive deterioration of the material at this salinity concentration (Fig. 1a).

The fragments of *C. sertularioides* cultivated at different salinity concentrations produced growth of the existing stolons and new stolons, except at 15 ppt salinity (Fig. 1b). The highest stolon growth rates were observed at salinity concentrations of 25 and 30 ppt, with average values of 2.638 ± 0.712% d^{-1} and 3.177 ± 1.305% d^{-1}, respectively (mean ± SD, n = 18). The lowest growth rates were observed at 15 ppt salinity (1.616 ± 0.760% d^{-1}).

Table 1. ANOVA results of differences in RGR (% d^{-1}) of *C. sertularioides* fragments under different salinity ranges under laboratory conditions.

	Biomass				
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Salinity	4	176.8	44.20	15.54	1.89×10^{-9}
Time	1	0.03	0.03	0.011	0.9141
Salinity/Time	4	2.37	0.59	0.209	0.9327
Residuals	80	227.4	2.84		
	Stolon length				
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Salinity	4	136.1	34.04	6.34	0.000175***
Time	1	0.31	0.30	0.05	0.8114
Salinity/Time	4	22.3	5.58	1.04	0.3917
Residuals	80	429.5	5.36		

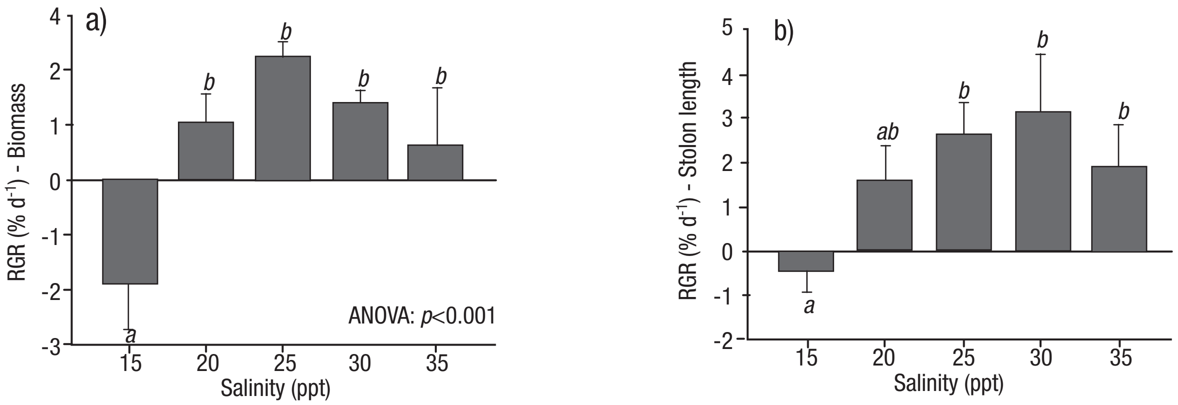
Significant codes (***) = 0, (**) = 0.001, (*) = 0.01, (.) = 0.05. Significant difference = 0.01.

The appearance of new fronds and rhizomes was observed at all evaluated salinities, excepting 15 ppt salinity. The highest number of new fronds (mean = 2.111 ± 0.787) and rhizomes (mean = 5.111 ± 1.109) was obtained at 25 ppt. The lowest number of new fronds (mean = 1.111 ± 0.192) and rhizomes (mean = 1.167 ± 0.500) was obtained at 35 ppt.

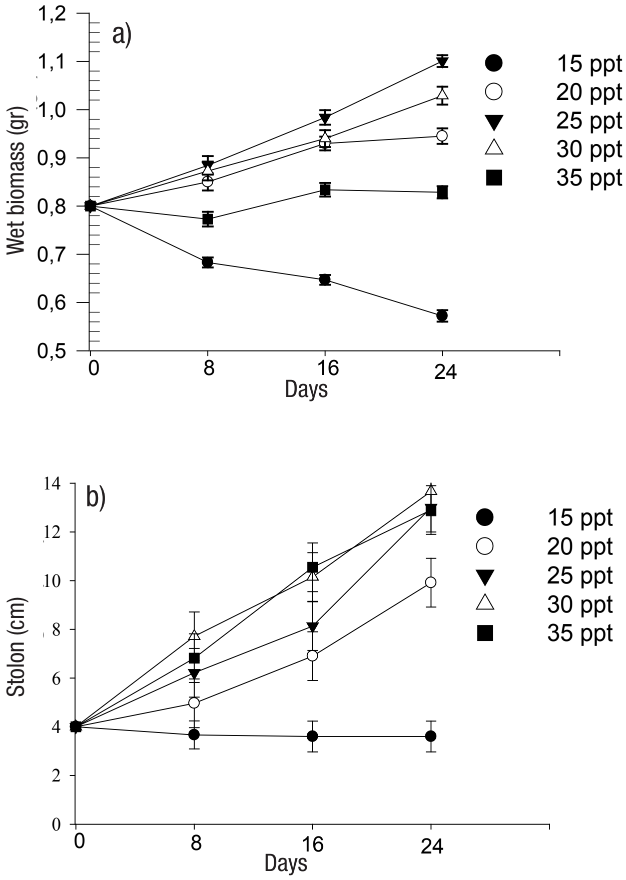
The daily growth rate, determined at three time intervals (Fig. 2), showed that, from the first week of culture, the relative growth rate of *C. sertularioides* varied under the different salinity concentrations evaluated. This behavior was constant during the culture period and was more obvious at salinities of 25 ppt and 30 ppt than at 15 and 35 ppt. During the 24 days of culture, growth rates of 4.82% d^{-1} and 3.02% d^{-1} were recorded at salinities of 25 and 30 ppt, respectively. At salinities of 20 and 35 ppt, growth rates of only 2.8% d^{-1} and 2.6% d^{-1} were observed.

DISCUSSION

According to these experimental results, *C. sertularioides* growth was significantly affected by changes in salinity. Growth increased with salinities over 20 and up to 30 ppt; the best growth response was obtained at 25 ppt. Variations in salinity can significantly affect the growth, distribution, and productivity of macroalgae (Chesnes & Montague, 2001). These results are consistent with the natural habitat of *C. sertularioides* in Tumaco Bay (Nariño, Colombia), where it is found in areas with average salinities of 24 ppt during its annual cycle (Fig. 3). Indeed, higher biomass of *C. sertularioides* showed a direct relationship with seasonal variation of salinity in the study area (Marin & Peña, 2014). Salinity is clearly one of the key variables influencing abundance and distribution of macroalgal meadows in shallow coastal environments, and it is the factor most easily manipulated through management decisions (Biber & Irlandi, 2006; Pérez-Ruzafa *et al*., 2012; Lirman *et al*., 2014).



Figures 1a-b. Effect of salinity on Relative Growth Rate (% d^{-1}) of *C. sertularioides*. **a)** Biomass. **b)** Stolon length. Means and standard deviations are shown (n = 18). Different letters represent significant differences between salinities as shown by Tukey´s test, p <0.05.



Figures 2a-b. Growth of *C. sertularioides* at different salinities (ppt). a) Increase in wet biomass (g). b) Increase in stolon length (cm). Error bars show SD ($n = 18$).

Results of this study showed a progressive deterioration of *C. sertularioides* fragments at 15 ppt of salinity, demonstrating a negative growth rate in terms of biomass and stolon growth (Mosquera-Murillo, 2012). Other species of the *Caulerpa* genus, such as *C. taxifolia* (West & West, 2007) and *C. lentillifera* J. Agardh (Guo *et al.*, 2015), exhibit reduced chlorophyll content and decreased Fv/Fm values, which could be the result of a disorganization of the cellular structure and chloroplasts in turgid cells. The rapid growth of *C. sertularioides* at salinities above 20 ppt observed in this study, as well as its deterioration at lower salinities, has also been reported for other species in this genus, such as *C. taxifolia* (Biber & Irlandi, 2006; West & West, 2007; Theil *et al.*, 2007).

The fragments of *C. sertularioides* grown at higher salinity concentrations (35 ppt) also showed low growth rates (0.618 ± 1.047 % d^{-1}), but maintained normal coloration. According to Kirst (1990), growth can be reduced near the salinity tolerance level in order to maintain osmotic regulation, which can guarantee survival. The reduction in growth can also be a consequence of the cumulative effect of enzymes and the reduction of turgidity pressure that inhibits cellular division (Lee & Liu, 1999; Liu *et al.*, 2000; Kamer & Fong, 2000). West and West (2007) reported optimal growth rates of *C. taxifolia* at salinities between 22.5 and 30 ppt, with null growth at lower salinities. (Liu & Phang, 2010). Increases and decreases in salinity generate stress in macroalgae, and species that are tolerant to these conditions present different strategies for growth (Liu *et al.* 2000; Ospina *et al.*, 2006; Choi *et al.*, 2010; Guo *et al.*, 2015).

These initial laboratory experiments demonstrated the effect of salinity changes on growth of *C. sertularioides*, and suggest that a range of experiments investigating other environmental factors, such as temperature, light, and nutrient conditions, would be beneficial in understanding the distribution of this species in the region.

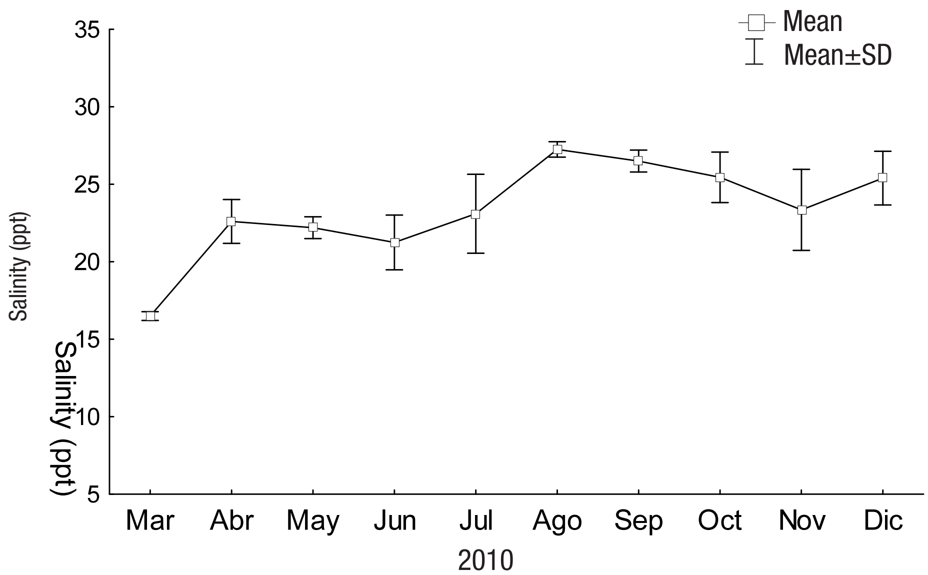


Figure 3. Salinity values recorded at sampling locations in Tumaco Bay (Nariño, Colombia), during 2010 (Marin & Peña, 2014).

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REFERENCES

Anderson, R. J., G. J. Levitt & A. Share. 1997. Experimental investigations for the mariculture of Gracilaria in Saldanha Bay, South Africa. *Journal of Applied Phycology* 8: 421-430. DOI: 10.1007/BF02178587

Areces, J. A. 1995. Cultivo comercial de carragenófitas del género Kappaphycus Doty. *In*: K. Alveal, M. E. Ferrario, E. C. Oliveira & E. Sar, (eds.) *Manual de métodos ficológicos*. Universidad de Concepción, Concepción, Chile, pp. 529-550.

Biber, P. & E. A. Irlandi. 2006. Temporal and spatial dynamics of macroalgal communities along an anthropogenic salinity gradient in Biscayne Bay (Florida, USA). *Aquatic Botany* 85: 65-77. DOI: 10.1016/j.aquabot.2006.02.002

Burfeind, D. & J. W. Udy. 2009. The effects of light and nutrients on Caulerpa taxifolia and growth. *Aquatic Botany* 90: 105-109. DOI:10.1016/j.aquabot.2008.06.004

Chesnes, T. C. & C. L. Montague. 2001. The effects of salinity fluctuation on the productivity and osmoregulation of two seagrass species. *Estuarine Research Federation Conference*. November 4–8., St. Petersburg, Florida.

Choi, H. G., Y. S. Kim, J. H. Kim, S. J. Lee, E. J. Park, J. Ryu & K. W. Nam. 2006. Effects of temperature and salinity on the growth of *Gracilaria verrucosa* and *G. chorda,* with the potential for mariculture in Korea. *Journal of Applied Phycology* 18: 269-277. DOI: 10.1007/s10811-006-9033-y

Choi, T. S., E. J. Kang, J. Kim & K. Y. Kim. 2010. Effect of salinity on growth and nutrient uptake of *Ulva pertusa* (Chlorophyta) from an eelgrass bed. *Algae* 25(1): 17-26. DOI: 10.4490/algae.2010.25.1.017

Eggert, A., U. Nitschke, J. A. West, D. Michalik & U. Karsten. 2007. Acclimation of the intertidal red alga *Bangiopsis subsimplex* (Stylonematophyceae) to salinity changes. *Journal of Experimental Marine Biology and Ecology* 343:176-186. DOI: 10.1016/j.jembe.2006.11.015

Glardon, C. G., L. J. Walters, P. F. Quintana-Ascencio, L. A. McCauley, W. T. Stam & J. L. Olsen. 2008. Predicting risks of invasion of macroalgae in the genus Caulerpa in Florida. *Biological Invasions* 10:1147-1157. DOI: 10.1007/s10530-007-9192-z

Goulard, F., M. Diouris, G. Quere, E. Deslandes & J. Y. Floćh. 2001. Salinity effects on NDP-sugars, floridoside, starch, and carrageenan yield, and UDP-glucose-pyrophophorylase and -epimerase activities of cultivated Solieria chordalis. *Journal of Plant Physiology* 158:1387-1394. DOI: 10.1078/0176-1617-00569

Guo H., J. Yao, Z. Sun & D. Duan. 2015. Effect of temperature, irradiance on the growth of the green alga Caulerpa lentillifera (Bryopsidophyceae, Chlorophyta). *Journal of Applied Phycology* 27: 879-885. DOI: 10.1007/s10811-014-0358-7

Kamer, K. & P. Fong. 2000. A fluctuating salinity regime mitigates the negative effects of reduced salinity on the estuarine macroalga, *Enteromrpha intestinalis* (L.) link. *Journal of Experimental Marine Biology and Ecology* 254: 53-69. DOI: 10.1016/S0022-0981(00)00262-8

Khou, M., N. A. Paul, J. T. Wright & P. D. Steinberg. 2007. Intrinsic factors influence the attachment of fragments of the green alga *Caulerpa filiformis*. *Journal of Experimental Marine Biology and Ecology* 352: 331-342. DOI: 10.1016/j.jembe.2007.08.010

Kirst, G. O. 1990. Salinity tolerance of eukaryotic marine algae. *Annual Review of Plant Physiology and Plant Molecular Biology* 41: 21-53. DOI: 10.1146/annurev.pp.41.060190.000321

Klüser, S., P. Peduzzi, G. Giuliani & A. De Bono. 2004. Caulerpa taxifolia*, a growing menace for the temperate marine environment.* Coll. Early Warning on Emerging Threats, UNE/DEWWA-Europe/GRID-Geneva, 4 p.

Lapointe, B. E. & B. J. Bedford. 2010. Ecology and nutrition of invasive *Caulerpa brachypus* f. *parvifolia* blooms on coral reefs off southeast Florida, U.S.A. Harmful Algae 9: 1-12. DOI: 10.1016/j.hal.2009.06.001Lee, T. M. & C. H. Liu. 1999. Correlation of decreased calcium contents with proline accumulation in the marine green macroalga *Ulva fasciata* exposed to elevated NaCl contents in seawater. *Journal of Experimental Botany* 50: 1855-1862. DOI: 10.1093/jxb/50.341.1855

Lirman, D., T. Thyberg, R. Santos, S. Schopmeyer, C. Drury L. Collado-Vides, S. Bellmund & J. Serafy. 2014. SAV Communities of Western Biscayne Bay, Miami, Florida, USA: Human and Natural Drivers of Seagrass and Macroalgae Abundance and Distribution Along a Continuous Shoreline. *Estuaries and Coasts* 37: 1243-1255. DOI: 10.1007/s12237-014-9769-6

Liu, C. H., M. C. Shih & T. M. Lee. 2000. Free proline levels in *Ulva* (Chlorophyta) in response to hypersalinity: elevated NaCl in seawater versus concentrated seawater. *Journal of Phycology* 36:118-119. DOI: 10.1046/j.1529-8817.2000.99127.x

Liu, F. & S. J. Phang. 2010. Stress tolerance and antioxidant enzymatic activities in the metabolisms of the reactive oxygen species in two intertidal red algae *Grateloupia turuturu* and *Palmaria palmate*. *Journal of Experimental Marine Biology and Ecology* 382: 82-87. DOI: 10.1016/j.jembe.2009.11.005

Marín, H. & E. Peña. 2014. Variación espacio-temporal de la biomasa del alga *Caulerpa sertularioides* en poblaciones naturales y en condiciones de cultivo en estanques de camarón en la Bahía de Tumaco, Pacífico Colombiano. *Boletín de Investigaciones Marinas y Costeras* 43: 121-135.

Marinho-Soriano, E., C. Morales & W. Moreira. 2002. Cultivation of *Gracilaria* (Rhodophyta) in shrimp ponds effluents in Brazil. *Aquaculture Research* 33: 1081-1086. DOI: 10.1046/j.1365-2109.2002.00781.x

Mosquera-Murillo, Z. 2012. Factores reguladores del crecimiento del alga verde Caulerpa sertularioides (Caulerpales, Chlorophyta) en condiciones de campo y laboratorio. Tesis de Maestría en Ciencias Biología. Facultad de Ciencias Naturales y Exactas. Universidad del Valle. Colombia. 95 p.

Ospina, N., E. J. Peña & R. Benítez. 2006. Efecto de la salinidad en la capacidad de bioacumulación de plomo en el alga verde *Rhizoclonium riparium* (Roth) Harvey (Chlorophyceae, Cladophorales). *Actualidades Biológicas* 28: 17-25.

Peña, E. J. 1998. Physiological ecology of mangrove associated macroalgae in a tropical estuary (Doctoral dissertation). University of South Carolina, USA. 59 p.

Peña, E. J., R. Zingmark, & C. Nietch. 1999. Comparative photosynthesis of two species of intertidal epiphytic macroalgae on mangrove roots during submersion and emersion. *Journal of Phycology* 35:1206-1214. DOI: 10.1046/j.1529-8817.1999.3561206.x

Peña, E. J. 2008. Dinámica espacial y temporal de la biomasa algal asociada a las raíces de mangle en la Bahía de Buenaventura, costa pacífica de Colombia. *Boletín de Investigaciones Marinas y Costeras* 37: 55-70.

Pérez-Ruzafa, A., C. Marcos, C. M. Bernal, V. Quintino, R. Freitas, A. M. Rodrigues, M. García-Sánchez & I. M. Pérez-Ruzafa. 2012. *Cymodocea nodosa* vs. *Caulerpa prolifera*: Causes and consequences of a long term history of interaction in macrophyte meadows in the Mar Menor coastal lagoon (Spain, southwestern Mediterranean). *Estuarine, Coastal and Shelf Science*.110: 101-115. DOI: 10.1016/j.ecss.2012.04.004

Piazzi, L., G. Ceccherelli & F. Cinelli. 2001. Threat to macroalgal diversity: effects of the introduced green alga *Caulerpa racemosa* in the Mediterranean. Marine Ecology Progress Series 210:149-159. DOI: 10.3354/meps210149

Scrosati, R. 2001. Population dynamics of *Caulerpa sertularioides* (Chlorophyta: Bryopsidales) from Baja California, Mexico, during El Niño and La Niña years. *Journal of the Marine Biological Association of the United Kingdom* 81 (5):721-726. DOI: 10.1017/S0025315401004520

Sousa, A. I., I. Martins, A. I. Lillebo, M. R. Flindt & M. A. Pardal. 2007. Influence of salinity, nutrients and light on the germination and growth of *Enteromorpha* sp. spores. *Journal of Experimental Marine Biology and Ecology* 341: 142-150. DOI: 10.1016/j.jembe.2006.09.020

Tejada, C. 2002. Clima marítimo de la bahía de Tumaco, un caso de aplicación del sistema de modelado integral de zonas costeras para Colombia. Tesis de Maestría (MSc en Ciencias Tecnológicas para la Gestión de la Costa) Universidad de Cantabria, España. 44 p.

Tejada, C., L. Castro. A. Navarrete. T. Cardona, L. Otero, F. Afanador, A. Mogollón & W. Pedroza. 2003. *Panorama de la Contaminación Marina del Pacífico Colombiano*. Centro Control Contaminación del Pacífico Colombiano. Ed. DIMAR. Serie Publicaciones Especiales Vol. 3, San Andrés de Tumaco, 120 p.

Theil, M., G. Westphalen, G. Collings & A. Cheshire. 2007. *Caulerpa taxifolia* responses to hyposalinity stress. *Aquatic Botany* 87: 221-228. DOI: 10.1016/j.aquabot.2007.06.001

West, J. & H. Calumpong. 1988. Mixed-phase reproduction of *Bostrychia* (Ceramiales, Rhodophyta) in culture. I. *B. tenella* (Lamouroux) J. Agardh. *Japanese Journal of Phycology* 36: 292–310.

West, J. A. & D. L. McBride. 1999. Long-term and diurnal carpospore discharge patterns in the Ceramiaceae, Rhodomelaceae and Delesseriaceae (Rhodophyta). *Hydrobiologia* 298/299: 101-13. DOI: 10.1023/A:1017025815001

West, E. J. & R. J. West. 2007. Growth and survival of the invasive alga, *Caulerpa taxifolia*, in different salinities and temperatures: implications for coastal lake management. *Hydrobiologia* 577: 87-94. DOI: 10.1007/s10750-006-0419-2

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