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Living in a coastal lagoon environment: Photosynthetic and biochemical mechanisms of key marine macroalgae

Marta García-Sánchez [a,*], Nathalie Korbee [b], Isabel María Pérez-Ruzafa [c], Concepción Marcos [a], Félix L. Figueroa [b], Ángel Pérez-Ruzafa [a]

[a] Departamento de Ecología e Hidrología, Facultad de Biología, Campus de Espinardo, Regional Campus of International Excellence "Campus Mare Nostrum", Universidad de Murcia, Murcia 30100, Spain
[b] Departamento de Ecología y Geología, Facultad de Ciencias, Universidad de Málaga, Málaga 29071, Spain
[c] Departamento de Biología Vegetal I, Facultad de Biología, Universidad Complutense de Madrid, Madrid 28040, Spain

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ABSTRACT

The physiological status of *Cystoseira compressa*, *Padina pavonica* and *Palisada tenerrima* was studied by in vivo chlorophyll fluorescence, pigment content, stoichiometry (C:N), accumulation of UV photoprotectors and antioxidant activity; comparing their photosynthetic response in a coastal lagoon (Mar Menor) and in Mediterranean coastal waters. In general, the specimens reached their highest ETR_{max} in spring in the Lagoon, but in summer in the Mediterranean, coinciding with their maximum biomass peak. The species exhibited a dynamic photoinhibition. Except *C. compressa*, they showed a lower decrease in F_v/F_m and higher recovery rates in the Mediterranean populations when exposed to high irradiance. The higher salinity and temperature of the lagoon could impair the photoprotection mechanisms. The acclimation to lagoon environments is species-specific and involves complex regulatory mechanisms. The results underline the importance of N in repair, avoidance, quenching and scavenging mechanisms. In general, Lagoon specimens showed higher pigment concentration. Although xanthophylls play important photo-protective and antioxidant roles, the observed trend is more likely to be explained by the higher temperatures reached in the lagoon compared to Mediterranean. Therefore the studied photosynthetic and biochemical mechanisms can be effective not only for high irradiance, but also for higher temperatures in a climate change scenario, but are highly dependent on nutrient availability.

1. Introduction

Coastal lagoons are part of a continuum between continental and marine aquatic ecosystems and are characterised by being shallow and relatively isolated from the open sea by coastal barriers that provide some connecting channels or inlets, making them subject to natural constraints (Pérez-Ruzafa et al., 2011a). In lagoons, the heterogeneity in environmental conditions may respond to a complex pattern of gradients, which contribute to the high biodiversity and biological productivity housed in these environments (Alongi, 1998; Pérez-Ruzafa et al., 2011a). Strong physical and ecological gradients (UNESCO, 1981) make them dynamic systems controlled and subsidized by physical energies. So, most coastal lagoons correspond to the type of coastal ecosystem that is characterised by frequent environmental disturbance and environmental fluctuations (Barnes, 1980; Kjerfve, 1994).

Submerged macrophytes living in coastal lagoons thus have to cope with large and frequent changes in their environment by means of morphological, physiological and life-cycle adaptations (Brock, 1986; Menéndez and Comin, 1989; Menéndez et al., 2002). Marine macroalgae in shallow waters need mechanisms for short-term acclimation to these fast changes. The most important are those mechanisms involved in protecting PSII from photo-oxidative damage. Carotenoids, the xanthophyll cycle and non-photochemical quenching (NPQ) are central constituents of such protection mechanisms (Andersson et al., 2006). Moreover, the accumulation of other photoprotective and antioxidant compounds, such as UV screen photoprotectors with antioxidant activity, mycosporine-like amino acids (MAAs) and phenols, could also be important (Abdala-Díaz et al., 2006; Korbee et al., 2006).

The Mar Menor is a choked, relatively deep and hypersaline lagoon, with mean salinity ranging between 38.5 and 47.7 psu,

* Corresponding author. Tel.: +34 868 884326; fax: +34 868 883963.
E-mail address: martagarcia@um.es (M. García-Sánchez).

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while the salinity in the Mediterranean ranges between 31.4 and 40.7 psu. Although the lagoon is threatened by several pressures, with the detrimental impact on the natural community structure and dynamics increasing in recent decades, it still maintains high levels of water quality and well-structured assemblages. A description of the hydrographic characteristics and the effects of recent human activities can be found in Pérez-Ruzafa et al. (1991; 2005a). Spatial variations exist regarding isolation from the sea (or confinement), and a vertical zonation of macrophytes and other benthic assemblages (Pérez-Ruzafa et al., 2007, 2008), as well as a high spatial heterogeneity and temporal fluctuations in water column parameters (Pérez-Ruzafa et al., 2005b). Despite its relative oligotrophy compared with other coastal lagoons, nutrient concentrations in the Mar Menor are higher than in the studied coastal Mediterranean area. A comparison between the environmental conditions in the sampling stations can be found in Pérez-Ruzafa et al. (2007). Environmental stress gradients affecting algal assemblages in the Mar Menor have been reported in a previous study (García-Sánchez et al., 2012).

While a specific lagoon flora does not exist and most saline coastal lagoons contain typical coastal marine species (Pérez-Ruzafa et al., 2011b), there is a great heterogeneity in their species composition – very few species (7.3% of the total) are shared by more than 10 lagoons in the Atlanto-Mediterranean area (Pérez-Ruzafa et al., 2011c). Despite this, coastal lagoons have well differentiated algal assemblages in relation to the open coastal sea in regard to the relative abundance and distribution of their species (Pérez-Ruzafa et al., 2008).

Several previous studies have focused on the effect of temperature, salinity and irradiance on the physiological response of some macroalgal species (Connan and Stengel, 2011; Dawes et al., 1999; Eggert et al., 2007; Figueroa et al., 2014; Lüder et al., 2001; Menéndez et al., 2002; Zou and Gao, 2013). However, only some attempts have been made to evaluate the acclimation capacity of the same species living in different environments (Andersen et al., 2013; Eggert et al., 2006; Karsten et al., 1993; Ursi et al., 2003). Moreover, it is worth stressing that most of the previous studies were based on culture experiments and not on field measurements such as those carried out in the present work.

In this study, we examine the photosynthetic and biochemical mechanisms of three dominant marine key macroalgae living in the Mar Menor lagoon, where species are exposed to wider thermal ranges and higher salinity conditions than in marine Mediterranean ecosystems. The main objective is to determine whether there are differences at the physiological and biochemical level between populations of the same species living in these two environments with different environmental characteristics: lagoonal stress *vs* the conditions found in Mediterranean coastal waters.

2. Material and methods

2.1. Study sites

The Mar Menor is a hypersaline coastal lagoon, located in the southeast of Spain (37° 42′ N; 0° 47′ W), with a surface area of 135 km^2, a mean depth of 3.6 m and maximum depth of about 6 m. A dense meadow of the seaweed *Caulerpa prolifera* (Forsskål) J.V. Lamouroux covers both the central area of the lagoon and the shallow muddy zones of low hydrodynamism, while in sandy shallow bottoms at depths of between 0 and 2 m, there are sparse patches of the seagrass *Cymodocea nodosa* (Ucria) Asch. There are some areas of natural rocky bottoms around the islands located within the lagoon and some calcareous and volcanic outcrops, in addition to some artificial breakwaters, where photophilous rocky shore communities can grow (Pérez-Ruzafa et al., 2008).

Cabo de Palos study area (37° 38′N; 0° 42′W) is located close to the Cabo de Palos-Islas Hormigas Marine Protected Area and represents the northern boundary of the so called Almería-Orán front. It also presents a great diversity of rocky assemblages and well-preserved seagrasses meadows, mainly composed by *Posidonia oceanica* (L.) Delile and *C. nodosa*.

2.2. Biological material

Three macroalgae were selected to perform this study: *Cystoseira compressa* (Esper) Gerloff and Nizamuddin (Fucales, Phaeophyceae), *Padina pavonica* (Linnaeus) Thivy (Dictyotales, Phaeophyceae) and *Palisada tenerrima* (Cremades) Serio, Cormaci, G. Furnari and Boisset (Ceramiales, Rhodophyta). Species were chosen on the basis of their key ecological role in rocky photophilous habitats and for being present in both the Mar Menor lagoon and Mediterranean coastal systems.

The thick leathery *C. compressa* and *P. tenerrima* have complex morphology and thallus with cortical and medullar cells, while the corticated foliose *P. pavonica* presents a slightly calcified simple thallus.

C. compressa is present in the upper infralittoral zone of open coastal waters in the Mediterranean, while in the Mar Menor it dominates the infralittoral zone of the confined area of the lagoon, with higher environmental stability. *P. pavonica* can be found in the infralittoral zone both in the Mediterranean and in the Mar Menor lagoon. Finally, *P. tenerrima* inhabits the midlittoral zone along Mediterranean coasts, occupying the upper infralittoral in the lagoon.

2.3. Sample design

Specimens of *C. compressa*, *P. pavonica* and *P. tenerrima* were collected from six locations (S.1–S.6). These sampling stations were representative of three different environments: (1) the southern basin of the Mar Menor, considered the most isolated and confined area (Lagoon: S.1, S.2), (2) the zone influenced by the Mediterranean Sea, close to the main channels through which water exchange between the lagoon and the open sea takes place (Inlets: S.3, S.4) and (3) open coastal sites in Mediterranean Sea (Mediterranean: S.5, S.6) (Fig. 1). *C. compressa* was not found in the inlet locations while *P. pavonica* was only absent from one of the inlet stations (S.4).

Biological samples were collected in two seasons, summer 2010 and spring 2011, according to the period of maximal growth rates and maximal biomass values for the selected species in both environments (Hegazi, 1999; Pérez-Ruzafa et al., 2008, 2007).

Photosynthesis was measured *in situ* using a portable pulse amplitude modulation (PAM) fluorometer (Diving-PAM, Walz, Germany). Samples for biochemical analyses were collected and immediately frozen in liquid nitrogen and stored at −80 °C to analyse phenolic compounds, antioxidant activity and photosynthetic pigments. Samples for analysing mycosporine-like amino acids (MAAs) and internal C and N were kept desiccated until analysis.

2.4. Environmental parameters

Temperature and salinity in the water column were recorded monthly from January 2010 to December 2011 using a multiparametric probe (YSI 6600), and samples for analysing nutrient concentration were collected and transported to the laboratory in dark and cold conditions. Nitrate (NO_3^-), nitrite (NO_2^-), ammonium (NH_4^+) and orthophosphate (PO_4^{3-}) were determined using an