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Effects of an experimental heat wave on fatty acid composition in two Mediterranean seagrass species

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ABSTRACT

Global warming is emerging as one of the most critical threats to terrestrial and marine species worldwide. This study assessed the effects of simulated warming events in culture on two seagrass species, *Posidonia oceanica* and *Cymodocea nodosa*, which play a key role in coastal ecosystems of the Mediterranean Sea. Changes in fatty acids as key metabolic indicators were assessed in specimens from two geographical populations of each species adapted to different *in situ* temperature regimes. Total fatty acid (TFA) content and composition were compared in *C. nodosa* and *P. oceanica* from natural populations and following exposure to heat stress in culture. After heat exposure, individuals of *C. nodosa* and *P. oceanica* adapted to colder temperatures *in situ* accumulated significantly more TFA than controls. For both species, the proportion of polyunsaturated fatty acids (PUFA) decreased, and the percentage of saturated fatty acids (SFA) increased significantly after the heat treatment. These results highlight that populations of both species living at warmest temperatures *in situ* were more thermotolerant and exhibited a greater capacity to cope with heat stress by readjusting their lipid composition faster. Finally, exposure of seagrasses to warmer conditions may induce a decrease in PUFA/SFA ratio which could negatively affect their nutritional value and generate important consequences in the healthy state of next trophic levels.

1. Introduction

Anthropogenic activity has rapidly increased greenhouse gasses concentration in the atmosphere over the last decades. Global warming is a direct consequence of such gas emissions and has emerged as a threat for terrestrial and marine species worldwide (Cheung et al., 2009; Pounds et al., 2006). Over recent years, anomalous summer heat waves have been recorded from the Mediterranean Sea, with sea water temperatures exceeding 28 °C in 2003 and 2006 (Marbà and Duarte, 2010). Marine heat waves are generally defined as prolonged discrete anomalously warm water events that can be described by their duration, intensity, rate of evolution, and spatial extent (Hobday et al., 2016). Projected environmental changes predict an increase in such extreme events in number and intensity over this century, with anticipated increases in average summer seawater temperatures by 4–5 °C (IPCC, 2014). These potential scenarios may alter the metabolism, growth and life cycle of marine foundation species (Pörter and Farrell, 2008; Hoegh-Guldberg and Bruno, 2010) and also the ecological interactions among associated communities, including seagrass systems (Post and Pedersen, 2008). With some native primary producers already living at their thermal upper limit, future climate change may compromise their survival, with dramatic effects on Mediterranean ecosystem functioning (Meehl and Tebaldi, 2004). Future projections estimate that Mediterranean ecosystems will experience the largest change in biodiversity worldwide resulting in conditions less favourable for native seagrasses and but more favourable for tropical species (Parry, 2000; Sala, 2000; Moschella, 2008).

Seagrasses are clonal marine plants dominating in tropical and temperate marine coastal ecosystems, providing ecologically relevant goods and services such as food, nursery habitats, sediment stabilization enhancing water quality and shoreline protection, and sequestration of atmospheric CO_2 into sediments (Orth et al., 2006; Nordlund et al., 2017). Their distribution is experiencing a global regression due to human impacts (Waycott et al., 2009), in particular since they prefer

Abbreviations: FA, fatty acids; EFA, essential fatty acids; PUFA, polyunsaturated fatty acids; SFA, saturated fatty acids; MUFA, monounsaturated fatty acids; FAME, fatty acid methyl esters; SST, sea surface temperature

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shallow and sheltered coastal areas which are threatened by global change. *Posidonia oceanica* and *Cymodocea nodosa* are the dominant seagrass species in coastal Mediterranean ecosystems with contrasting biological attributes and ecological strategies. The endemic *P. oceanica* is the most dominant species in infralittoral bottoms to a maximum depth of 25–40 m (Procaccini et al., 2003). It is a large, long-lived (Arnaud-Haond, 2012) seagrass with low growth and recovery rates (Duarte et al., 2006), making it particularly vulnerable to environmental disturbances. Declines in the extent of *P. oceanica* meadows have been reported elsewhere mainly caused by anthropogenic impacts of coastal development (Marbá et al., 2005; Boudouresque et al., 2009; Díaz-Almela et al., 2009). *C. nodosa* is the second most abundant seagrass in Mediterranean Sea, and its distribution ranges from the Iberian Peninsula to Senegal and Cape Verde. It is a species adapted to a wide range of coastal habitats with contrasting regimes of salinity, temperature and nutrients, from the open sea to semi-enclosed coastal lagoons. Compared to *P. oceanica*, it is smaller in size, with higher growth rates, high phenotypic plasticity and rapid recovery such as from temperature disturbances (Olesen et al., 2002; Duarte et al., 2006; Sandoval-Gil et al., 2014). In the summer of 2003, Mediterranean seagrass meadows were exposed to an extreme heat wave episode leading to reduced recruitment rates and hence increased mortality (Balearic Islands, Marbà and Duarte, 2010; Jordà et al., 2012) and inducing massive flowering (Diaz-Almela et al., 2007). Responses of *C. nodosa* to heat stress are less well studied but are rather variable and less severe than those of *P. oceanica* (Olsen et al., 2012; Marín-Guirao et al., 2016; Tutar et al., 2017).

Primary producers play a key role biosynthesising the majority of essential fatty acids (Behrens and Kyle, 1996; Dalsgaard et al., 2003) which are subsequently transferred to higher trophic levels. Lipid metabolism and fatty acid synthesis play an important role in the membrane structure and energy storage in plants and algae (Rabbani et al., 1998; Mendoza et al., 1999; Klyachko-Gurvich et al., 1999). Polyunsaturated fatty acids (PUFA) are mainly partitioned into structural lipids (glycolipids and phospholipids) constituting the cellular membranes, in particular the thylakoid membranes of chloroplasts, promoting their fluidity, the electron transport, and therefore the photosynthetic activity (Gombos et al., 1994; Sanina et al., 2008). By contrast, saturated fatty acids (SFA) are mainly partitioned into triacylglycerols (TAG) as storage compounds. Lipids and fatty acids have been largely studied in microalgae, seaweeds, lichens and terrestrial plants, however, to a lesser extent in marine plants (Khotimchenko et al., 2002; Sanina et al., 2004). In aquatic plants, fatty acid metabolism is strongly regulated by environmental factors (Viso et al., 1993) and changes in sea surface temperature can be expected to affect fatty acid composition of seagrasses (Lee et al., 2007). To date, fatty acids in seagrasses have been mainly evaluated as qualitative markers for marine trophic relationships between species (Auel et al., 2002).

At the base of the marine food web, primary producers represent the main source of food, as well as essential PUFA (Iken et al., 1998). Since seagrasses constitute an essential part of herbivores diet, future warming may affect their nutritional value, and therefore the health of potential grazers *via* dietary intake (Havelange et al., 1997). Recent studies showed that future scenarios of climate change may induce changes in seagrass leaf composition, such as pigments concentration, and generate changes in the herbivore diet preferences (Hernán et al., 2017; Beca-Carretero et al., 2017). Previous studies in marine primary producers observed an increase of PUFA levels with a decrease of temperature (Gosch et al., 2015; Schmid et al., 2017a). Hence, decreases in PUFA levels and in PUFA/SFA ratios are anticipated under future warming. Therefore, further detailed analyses of the role of fatty acid metabolism as potential adaptive mechanism of marine plants to heat stress and hence, to future climate change scenarios, are required. However, potential effects of stress caused by heat waves on lipid metabolism in seagrasses have not been evaluated experimentally.

In this study, the effects of simulated warming events were investigated in a mesocosm system to assess changes in key metabolic indicators, such as fatty acids, in specimens from two geographical (northern and southern) populations of *P. oceanica* and *C. nodosa* adapted to different *in situ* temperature regimes. Total fatty acid content and composition were determined after exposure to heat treatment for six weeks, and again following six subsequent weeks of recovery. Moreover, the variation in the proportion of PUFA and PUFA/SFA ratios in seagrasses from across their geographical distribution range in relation to *in situ* annual seawater surface temperatures (SST) were assessed. Finally, the ecological implications of changes in fatty acid composition under potential future warming scenarios in higher trophic levels are discussed.

2. Methods

2.1. Experimental setup

In June 2016, large fragments of rooted *Posidonia oceanica* and (Linnaeus) Delile, and *Cymodocea nodosa* (Ucria) Ascherson bearing apical growth meristems and a large number of connected shoots were collected by divers in two Mediterranean regions of Spain at 5–7 m depth: the northern populations were located in Catalonia (42° 06′23″N, 3° 10′ 16″E), such as *P. oceanica* in Cala Montgó and *C. nodosa* in Ebro Delta, and the southern populations in the Murcia region (37°34′20.8″N, 1° 12′28.1″W). These two regions are about 700 km apart, displaying substantial differences in SST of about 6 °C in summer

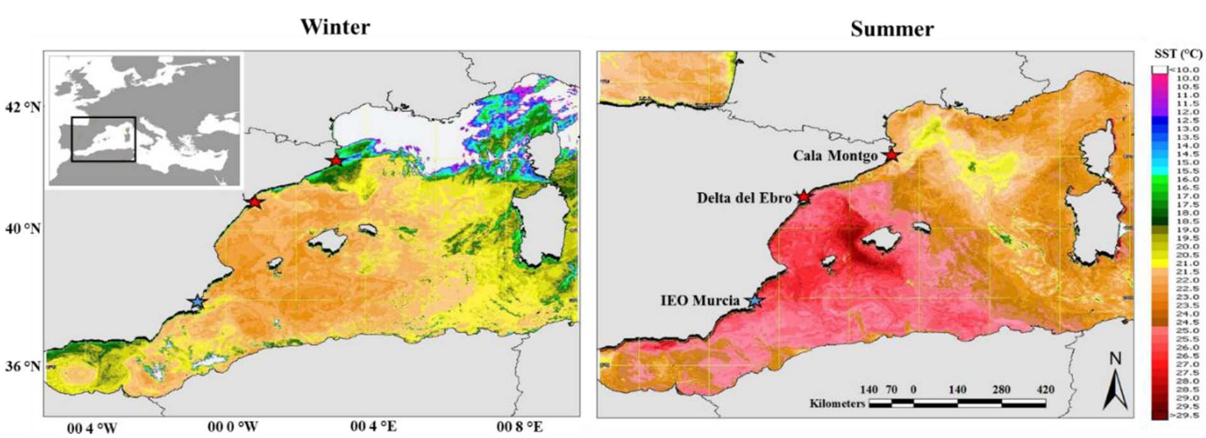

Fig. 1. Map of satellite-derived data of winter and summer sea surface temperatures (SST) (http://www.ieo-santander.net) in the western Mediterranean Sea with the location of the two sites where the samples were collected (red stars), two Catalonia, Cala Montgo and Delta del Ebro. IEO Murcia is the location where the experiments were conducted (blue star). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)